Investigation of Population Abundance, Distribution, and Population Linkage of Indo-Pacific Bottlenose Dolphins (*Tursiops aduncus*) on the North and South of Zanzibar Using Mark-Recapture and Acoustic Methods

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Table of Contents

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Abstract

Previous studies, using a variety of methods such as photographic identification, fisheries observer programs, or genetic testing, on Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Zanzibar Island, Tanzania, suggest separate populations around the north and south coasts. However, most research around the island has focused on the south coast, and movement of dolphins around the coastline is poorly understood. Photographic identification data, consisting of dorsal fin images, and acoustic data from dolphin whistles, both collected in 2008, were analysed to examine linkages between north and south Zanzibar. Photographic identification data was applied in a Mark-Recapture framework, using open population models, to generate abundance estimates of 149 (95% CI 128-173) and 120 (95% CI 97-149) individuals for the north and south coasts of Zanzibar respectively. As 16 individuals had moved from the south to the north coast of Zanzibar during the two month study, a combined population estimate of 353 (95% CI 290-430) individuals for Zanzibar Island was also generated. Acoustic analysis of standard whistle parameters was used to investigate whether these learned signals shared features between the putative populations, using whistle data collected in Plettenberg Bay, South Africa as an out-group. Discriminant function analysis of whistle parameters indicated high classification success of whistles recorded from animals in the north location (86.2%), moderate classification success for the outgroup (61.8%), and zero classification success for Zanzibar's south coast population. High misclassification rates for south Zanzibar suggest that these whistles cannot be readily discriminated from those of north Zanzibar. Shared whistle features suggest that learning may take place between individuals moving between localities. Coupled with previous genetic studies, this study suggests female philopatry and male mediated gene flow between the two areas; however, more genetic markers are necessary to test this interpretation. Further work is also necessary to quantify the degree of movement of dolphins around Zanzibar Island, and potential migration into the area, which will assist in developing management plans.

Keywords: photo-identification, dolphin whistles, discriminant function analysis, Huggins closed capture models, POPAN parameterization, Jolly-Seber framework, acoustic variation, population structure

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1. Introduction

The population status, and subsequent conservation decisions, regarding cetaceans requires information on population size and abundance trends, including distribution, behaviour, mortality, anthropogenic effects, and movement patterns (Gomez-Salazar, Trujillo, & Whitehead, 2011a; Stensland, Carlén, Särnblad, Bignert, & Berggren, 2006; Wilson, Hammond, & Thompson, 1999). Mark-Recapture (MR, also called capture-recapture or capture-mark-recapture) analysis using photographic identification (photo-identification) data has proven useful in obtaining abundance estimates for many different species, including cetaceans (Elwen, Reeb, Thornton, & Best, 2009; Hammond 1986; Stensland et al., 2006; Urian et al., 2015). Along with being used to obtain population estimates, photo-identification data itself, which involves identifying individuals based on photographs of certain natural markings (Würsig & Jefferson, 1990), can also provide insight into site fidelity, population structuring (Toth, Hohn, Able, & Gorgone, 2012; Tyson, Nowacek, & Nowacek, 2011), group composition, behaviour, and, if data are collected at more than one site, area distribution and movement patterns (see review in Würsig & Jefferson, 1990). Acoustic analysis of commonly produced calls, including dolphin whistles, has been used to accurately detect geographic variation in the whistle parameters of cetacean species (Gridley, Berggren, Cockcroft, & Janik, 2012; Hawkins, 2010; Wang, Würsig, & Evans, 1995b), which could give further insight into species distribution (McGregor, Peake, & Gilbert, 2000). Combining photo-identification and acoustic data may therefore provide information on population linkages.

Currently classified as data deficient by The IUCN Red List of Threatened Species, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) are likely not threatened on a global scale. However, due to their inshore distribution, local populations in certain areas may be significantly impacted by bycatch, habitat destruction, toxic effects from chemicals, boat traffic, marine construction, and reduced prey availability (Hammond et al., 2012). This is the case with the Indo-Pacific bottlenose dolphin population around Zanzibar Island, Tanzania, where, largely due to high bycatch rate and heavy tourism, they are regarded as threatened (Amir, 2010; Berggren, 2011).

The taxonomy of *Tursiops* spp. is not well resolved (Charlton-Robb et al., 2011; Natoli, Peddemors, & Hoelzel, 2004). At present, three different species are recognized: the common bottlenose dolphin (*T. truncatus*) (Leduc, Perrin, & Dizon, 1999; Natoli et al., 2004), Indo-Pacific bottlenose dolphin (*T. aduncus*) (Leduc et al., 1999; Wang, Chou, & White, 1999, 2000), and the Burrunan dolphin (*T. australis*) (Charlton-Robb et al., 2011). This study will use this currently accepted taxonomy, which lists coastal bottlenose dolphins from the south-west Indian Ocean as *Tursiops aduncus* (Best, 2007; Hammond et al., 2012; Natoli et al., 2004).

Tursiops aduncus are found in the warm-temperate to tropical coastal waters, typically in depths of < 50 m, of the far west Pacific Ocean and Indian Ocean, including Japan, China, Indonesia, Australia,

and Africa (Figure 1) (Best, 2007; Hammond et al., 2012; Natoli et al., 2004). They are the smallest of the three recognized species (Charlton-Robb et al., 2011), with males and females averaging 2.2 m in length and weighing 151 kg and 126 kg respectively (Amir, 2010), and are differentiated by having thinner, elongated beaks, more teeth, and ventral spotting (Best, 2007; Natoli et al., 2004; Perrin, Robertson, van Bree, & Mead, 2007). Although smaller in size, the whistle frequency parameters of *T. aduncus* tend to be lower than those of *T. truncatus* (Gridley et al., 2012; Hawkins, 2010). Females reach sexual maturity between 7-8 years, when they are between 1.90-2.00 m in length, whereas males reach sexual maturity at around 16 years, at a body length of 2.13 m (Amir, 2010). Indo-Pacific bottlenose dolphins calve year round, peaking between November and March (Amir, 2010). They have a 12.3 month gestation period and calve at an average interval of 2.7 years (Amir, 2010). Around Zanzibar Island, bottlenose dolphins prey on a wide number of species (50 different species of bony fish and 3 squid species), but fish are their main food source comprising 87% of the total prey mass (Amir, 2010). As little information regarding the abundance of these fish species around Zanzibar Island is available, it is not possible to determine whether these species are the most abundant and easiest to catch, but the ecology and behaviour of the prey species suggests that the dolphins hunt over both reef and sandy bottom areas close to the shore (Amir, Berggren, Ndaro, & Jiddawi, 2005). Although these prey species are not targeted by commercial fishermen, their habitats overlap with fish that are, increasing the risk of dolphins being caught in gillnets (Öhman, 2010).

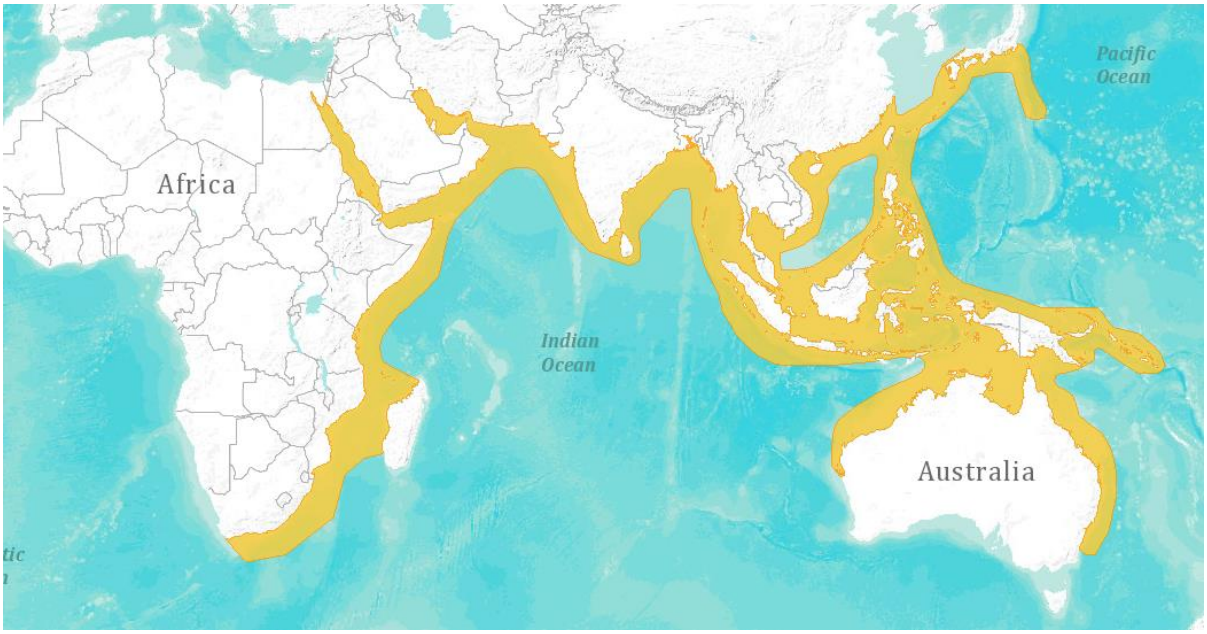

Figure 1: Worldwide distribution of *T. aduncus*. Map from: IUCN Red List of Threatened Species (Hammond et al., 2012).

1.1 Threats to Zanzibar's Bottlenose Dolphins

The Indo-Pacific bottlenose dolphin population around Zanzibar Island has long been an important resource for the people of the island. Prior to 1996, bottlenose dolphins were hunted off the south coast, mainly for use as shark bait, with 23 animals being taken in that final year of active dolphin take (Amir & Jiddawi, 2001). The earliest estimate of the bottlenose dolphin population around Zanzibar's south coast is from 1999 and was 150 (95% CI 142-172) individuals (Stensland et al., 2006). Therefore, in 1996, the final year of active dolphin hunting, around 15% of the total population were removed. Even in areas where there is no direct taking of marine mammals, indirect take, in the form of fishing bycatch, poses the most serious threat to their populations (Amir, Berggren, & Jiddawi, 2002; Read, Drinker, & Northridge, 2006; Schipper et al., 2008). This appears to be the case off the south coast of Zanzibar Island (hereafter referred to as "SZ" for south Zanzibar), where an estimated 9.6-11.8% removal rate, due to fishing bycatch (Amir, 2010), exceeds the assumed potential growth rate of < 4% (Moore & Read, 2008; Wade, 1998) and the designated potentially sustainable level of take of 2% (Berggren, 2011).

Although bycatch is likely the current main threat to the Zanzibar bottlenose dolphin population, threats from tourism also exist. Commercial tourism, involving taking tourists out to watch and swim with the dolphins, began in Zanzibar in 1992 (Amir & Jiddawi, 2001) and has been steadily growing ever since (Stensland & Berggren, 2007). Starting from just a few in 1992, the number of boats conducting dolphin tourism in SZ rose to 35 in 2001 (Amir & Jiddawi, 2001), and again to nearly 50 in 2007 (Ngazy, Jiddawi, & Amir, 2007). Activities associated with these boats include pulling up right next to the dolphins and having tourists enter the water to swim with the animals (Christiansen, Lusseau, Stensland, & Berggren, 2010). Tourism boats in SZ run year round, usually between 09:00 h and 15:00 h, constituting roughly 50% of daylight hours (Stensland & Berggren, 2007). Female dolphins were found to be interacting with tourism boats for roughly 43% of the day, and swimmers 28% (Stensland & Berggren, 2007). The number of tourism boats interacting with a group varies between one and 13 boats at a time, averaging 4 boats simultaneously, meaning that a single group of dolphins may be subjected to tourism boats and swimmers for several hours in a row (Christiansen et al., 2010). Although no formal rules are in place to regulate the dolphin tourism industry in Zanzibar (Amir & Jiddawi, 2001; Stensland & Berggren, 2007), some boat operators are aware of codes of conduct that should be followed, but only 60% say they follow these codes, and even then, only occasionally (Ngazy et al., 2007).

The high level of tourism in SZ is causing changes to the behaviour of the bottlenose dolphins (Christiansen et al., 2010; Stensland & Berggren, 2007). Specifically, Stensland and Berggren (2007) report that the dolphins spend less time resting, and travel for longer periods of time when subjected to tourism boats. They also found that females altered their movement patterns when more than two

boats were present and dove more frequently when swimmers were in the water. Christiansen et al. (2010) report that dolphin tourism in Zanzibar results in the dolphins spending less time foraging, resting, and socializing, and more time travelling, even with a tourism intensity consisting of only 10% of daytime hours. Similar increases in time spent travelling has been estimated to lead to a substantial decrease in energy intake amongst killer whales (*Orcinus orca*) (Williams, Lusseau, & Hammond, 2006), and bottlenose dolphins are likely to be similarly affected.

These behavioural changes can have potentially deleterious effects on the bottlenose dolphin population (Bejder, 2005; Bejder et al., 2006; Christiansen et al., 2010; Stensland & Berggren, 2007). Bejder (2005) found that disturbances due to boat activity lead to decreased reproductive success amongst cetaceans. Stensland and Berggren (2007) also provide strong evidence that because calves nurse during resting times, frequent tourism boats interrupting the animals' resting time could lead to less nursing time. This may have a domino effect, negatively affecting the survival probability of calves, as found by Bejder (2005). Combined with a potential interruption of sexual behaviours, also associated with socialising (Christiansen et al., 2010), this could lead to fewer offspring as well as lower offspring survival rate. A decline in dolphin abundance due to tourism boats has already been found in a population of bottlenose dolphins in Shark Bay, Australia (Bejder et al., 2006). This study showed that when the number of tourism boats reached two, there was a decrease in population size of around 14%. This could be potentially devastating to a small population, such as the one around SZ. Due to the dangers associated with heavy tourism use and high rate of bycatch, the conservation status of bottlenose dolphins around Zanzibar should be considered threatened (Berggren, 2011).

1.2 Previous Studies on North and South Zanzibar

Research on bottlenose dolphins around Zanzibar Island has been conducted mainly off the north and south coasts, rather than on the east and west coasts. There are a number of reasons for focusing on these two coasts. Firstly, bottlenose dolphins occur year round around the south (Amir & Jiddawi, 2001) and north (Amir, Jiddawi, & Berggren, 2005) coasts. Secondly, photo-identification data indicates the existence of a resident population on the south coast (Stensland et al., 2006). Finally, although bottlenose dolphins off the north coast (hereafter referred to as "NZ" for "north Zanzibar") have not been studied as extensively as those in the south, Amir et al. (2002) and Amir, Jiddawi, and Berggren (2005) found that dolphin bycatch is mainly observed off the north coast, making it an important area of study. The higher bycatch numbers in NZ are likely the result of greater fishing effort (Amir, Jiddawi, & Berggren, 2005), as more fishing boats are present in this area than in other areas around the island (Amir et al., 2002).

Särnblad, Danbolt, Dalén, Amir, and Berggren (2011) examined mitochondrial DNA (mtDNA) from individuals in NZ and SZ, finding a significant difference between dolphins from the two areas (Φ_{ST} = 0.31, $P < 0.001$; F_{ST} = 0.19, $P = 0.002$). They concluded that although further research is needed to

confirm the findings, dolphins from the two areas should be considered separate because there is limited genetic exchange between them (Särnblad et al., 2011). The study also found little differentiation in the mtDNA between bottlenose dolphins from SZ and from South Africa, in spite of the large distances between sampling locations compared to NZ and SZ (Särnblad et al., 2011).

Previous bottlenose dolphin abundance estimates were performed using MR techniques on photo-identification data from the SZ area by Öhman (2010) and Stensland et al. (2006). Stensland et al. (2006) used a study area of 26 km^2, 1.7 km^2 of which was found to have the highest concentration of dolphins, and obtained estimates each year from 1999-2002. Estimates varied yearly, from a low of 136 (95% CI 124-172) dolphins in 2002, to a high of 179 (95% CI 167-212) individuals in 2001 (Stensland et al., 2006). Öhman (2010) expanded the study area to 270 km^2, and obtained estimates of 184 (95% CI 151-218) dolphins in 2004 and 212 (95% CI 163-260) dolphins in 2007. None of these estimates substantially differed from the others as the confidence intervals overlapped (Öhman, 2010; Stensland et al., 2006). Although the two most recent estimates were found to be higher than the four previous ones, this is likely explained by the increase in study area size. Öhman (2010) also obtained population estimates using only the 26 km^2 area used by Stensland et al. (2006), and obtained abundance estimates of 163 (95% CI 92-233) dolphins in 2004 and 139 (95% CI 124-182) in 2007.

An initial population estimate of 254 (95% CI 199-460) dolphins in NZ was reported by Berggren (2011), using the same photo-identification data, collected in 2008, as was used in this study (T. Gridley, personal communication, 2016); however, the exact method of obtaining this estimate is unclear. A preliminary analysis of the photo-identification data indicated that animals from SZ were travelling to NZ over relatively short time scales (within the two month study period), suggesting some degree of mixing between the groups (Berggren, 2011; Öhman, 2010). Additionally, a study involving analysis of the vocalizations of bottlenose dolphins from the two coasts also indicated that the two groups could be mixing (Gridley, 2010). These findings could potentially put into question whether separating the bottlenose dolphins from north and south Zanzibar into two distinct populations is appropriate.

1.3 Populations Structuring of *Tursiops* spp.

When discussing population structuring, it is important to define the term "population." A population consists of "units of interbreeding organisms with autonomous dynamics and recruitment" (Krützen, Sherwin, Berggren, & Gales, 2004). Determining population boundaries, or structures, within species is important for developing management policies (Krützen et al., 2004; Parsons et al., 2006; Toth et al., 2012; Tyson et al., 2011), and investigating the social structure (Krützen et al., 2004), ecology, evolution, and biology (Parsons et al., 2006; Toth et al., 2012) of the species. In the marine environment, investigating population structures is challenging because there are often no obvious

geographical boundaries. However, by studying differences in morphology, habitat selection, prey species, parasite loads, social structure, genetics, distribution (see review in Toth et al., 2012), and vocal characteristics (Hawkins, 2010; May-Collado & Wartzok, 2008; Morisaka, Shinohara, Nakahara, & Akamatsu, 2005b), population structures have been detected amongst many marine species.

Regarding bottlenose dolphins, separate populations of *Tursiops* spp. have been identified in a number of areas on both macrogeographic (a large portion of the species range) and microgeographic (relatively small) scales. In New Jersey, USA, photo-identification and distribution surveys were used to identify at least two stocks of common bottlenose dolphins (Toth et al., 2012). This work had been built on previous macrogeographic studies, which provided evidence of the need to divide *T. truncatus* along the east coast of North America into five different populations using genetic testing (Rosel, Hansen, & Hohn, 2009). Tyson et al. (2011) also used photo-identification data to divide *T. truncatus* in the area between St. Vincent Sound and Alligator Harbor in Florida, USA into two separate communities. Two separate communities have also been found in *T. truncatus* in the Moray Firth, Scotland, by analyzing social structure using photo-identification data (Lusseau et al., 2006). Genetic data was used to separate *T. truncatus* living within 250 km of each other in the Bahamas into three distinct subpopulations (Parsons et al., 2006).

Different populations of the same species have been found to differ in the calls, songs, and sounds they make over both macrogeographic and microgeographic distances. As they can provide indications around the extent of the isolation between groups, these differences in vocalisations can have important implications for conservation (McGregor et al., 2000). Mitani, Hunley, and Murdoch (1999) found that the calls of male chimpanzees (*Pan troglodytes schweinfurthii)* from two different populations differed in terms of the frequency of their calls and the lengths and rate of certain aspects of the calls. Cape Horseshoe Bats (*Rhinolophus capensis*) also differ in the frequencies of their echolocation calls between populations (Odendaal & Jacobs, 2011). Many bird species have been found to differ in song types and syllables, based on geographical location, including the Grey-cheeked Fulvetta (*Alcippe morrisonia)* (Shieh, 2004) and corn buntings (*Miliaria calandra*), which have been found to differ in their vocalisations on a microgeographic scale, even in an environment that is fairly homogenous and has no obvious barriers to dispersal (McGregor et al., 2000).

Population structures of *Tursiops* spp. separated by microgeographic distances have also been found by analyzing the differences in whistle characteristics between groups. Hawkins (2010) was able to differentiate between the whistles from two resident groups of *T. aduncus* in Australia. May-Collado and Wartzok (2008) studied *T. truncatus* whistles of two adjacent populations off Costa Rica and Panama, separated by only 35 km, and found, using a discriminant function analysis (DFA), that the whistle characteristics from the dolphins in the two areas were clearly distinct from each other. The

DFA was able to correctly classify 81.1% of Bocas del Toro (Panama) and 63.6% of Gandoca-Manzanillo (Costa Rica) whistles to the correct population (May-Collado & Wartzok 2008). In both of these studies, the whistles from the two populations were found to be more similar to each other than to populations separated by macrogrographic distances. This lead May-Collado and Wartzok (2008) to propose that there exists the potential for movement between the two areas, as was also proposed by Wang et al. (1995b) in a study of adjacent populations of *T. truncatus* in Texas, USA.

Hawkins and Gartside (2008) used photo-identification data to study home ranges, behavior, and social structure of *T. aduncus* in Byron Bay, Australia, and concluded that dolphins from two areas, separated by 55 km, should be considered as a single unit for management purposes. They further concluded that within this singular unit were two distinct resident groups of females (Hawkins & Gartside, 2008). In a study of bottlenose dolphins in Shark Bay Australia, Krützen et al. (2004) found two distinct haplotypes, based on analysis of mtDNA, representing two separate subpopulations. They also found that interbreeding between the two haplotype clades was occurring. Having found no intermediates, in spite of extensive sampling, Krützen et al. (2004) postulated that Shark Bay could have been colonized by bottlenose dolphins with two distinct mtDNA lineages.

Based on their findings, Krützen et al. (2004) concluded that female dispersal is far more limited than male dispersal amongst the bottlenose dolphins in Shark Bay, Australia, and that gene flow is likely male-mediated. Amongst terrestrial mammals, female philopatry, coupled with male-mediated gene flow, is common (Clutton-Brock, 1989). This has also been found to occur amongst other cetacean species including harbor porpoises (*Phocoena phocoena*) (Rosel, France, Wang, & Kocher, 1999; Wang, Gaskin, & White, 1996), beluga whales (*Delphinapterus leucas*) (Brown Gladden, Ferguson, & Clayton, 1997), and narwhals (*Mondon monoceros*) (Palsbøll, Heidi-Jørgensen, & Dietz, 1997). The evidence of genetic differentiation between NZ and SZ, based on mtDNA analysis, is indicative of limited genetic exchange of reproducing females between NZ and SZ (Särnblad et al., 2011). However, the same study found low nucleotide divergence (0.68%) among the Zanzibar haplotypes, which does not support the argument of no gene flow between NZ and SZ (Särnblad et al., 2011).

1.4 Mark-Recapture and Photographic Identification

Mark-Recapture studies involve marking individuals and comparing the proportion of those individuals recaptured in subsequent samples to generate an estimate of abundance or survival (Hammond, 1986; Stensland et al., 2006; Wilson et al., 1999). Traditionally, these studies have been carried out by physically capturing an individual and marking it in some way: painting, tagging, or altering the animal's appearance (Hammond, 1986). Photographic identification using natural markings to identify individuals, including scars, notches, and nicks on the dorsal fins of bottlenose dolphins (Würsig & Jefferson, 1990; Würsig & Würsig, 1977), has proven to be an efficient alternative to tagging animals, particularly with the improvements in digital photo technology in the

last two decades (Gomez-Salazar et al., 2011a; Urian et al., 2015). In addition to being used to obtain abundance estimates through MR analysis, photo-identification data can also be used to provide insight into migrations, group composition, area distribution, behavioural patterns, habitat use, and, if data is collected over a long time span, life history information including calving intervals, age at sexual maturity, life span, and disease and mortality rates (see review in Gomez-Salazar et al., 2011a; Williams, Dawson, & Slooten, 1993; Würsig & Jefferson, 1990).

Photographic identification data are pictures taken of a specific area of an individual. The area that is to be targeted varies from species to species, and is chosen to most accurately recognize an individual's distinctive markings in subsequent pictures. The choice of the area to be targeted is based on the longevity and changeability of the marks on those areas (Würsig & Jefferson, 1990). Marks that do not last for a long time, or that change dramatically over time, are not chosen because photo-identification studies can occur over many years, and individuals must be recognizable throughout (Urian, Hohn, & Hansen, 1999; Würsig & Jefferson, 1990). The target areas differ for different species and can include callosity patterns in southern right whales (*Eubalaena australis*) (Carroll et al., 2011), tail flukes in humpback whales (*Megaptera novaengliae*) (Minton et al., 2011), pelage patterns on snow leopards (*Uncia uncia*) (Jackson, Roe, Wangchuk, & Hunter, 2006), scarring in sea otters (*Enhydra lutris*) (Gilkinson, Pearson, Weltz, & Davis, 2007), and patterns of lines and spots on whale sharks (*Rhincodon typus*) (Holmberg, Norman, & Arzoumanian, 2009). In bottlenose dolphins, it is the dorsal fin that is targeted (Würsig & Jefferson, 1990; Würsig & Würsig, 1977) because they are frequently marked in some way. They could be irregularly shaped, or show deformities including nicks, notches, or scars (Urian et al., 2015; Würsig & Jefferson, 1990; Würsig & Würsig, 1977). Due to the trailing edge of the dorsal fin having thin, non-regenerating tissue (Würsig & Würsig, 1977), these marks likely last for life and are therefore sufficiently long-lasting for use in photo-identification studies (Würsig & Jefferson, 1990). As these markings are obtained through incidental events, the patterns often vary greatly between individuals (Karczmarski & Cockcroft, 1998). Additionally, in most bottlenose dolphin populations, over 50% of individuals are identifiable using these markings (Würsig & Jefferson, 1990). Therefore, the markings on the trailing edge of the dorsal fins of bottlenose dolphins are effectively used to identify individual dolphins.

Identification through natural markings has some disadvantages, such as it being easier to make false identifications due to marks changing over time, or twinning, where two or more individuals have marks similar enough to be identified as the same individual (Hammond, 1986). These potential shortcomings, and how to overcome them, are discussed in section 2.3.1. However, the obvious advantages of not having to physically handle the animals, certainty that the markings will not fall off, and that markings do not stress the animals or affect either their behaviour or future catchability, make photo-identification data effective for use with cetacean MR studies (Gomez-Salazar et al., 2011a; Hammond, 1986; Würsig & Jefferson, 1990).

1.4.1 Assumptions for Mark-Recapture Analysis

Two broad types of MR models are commonly used for photo-identification studies of cetaceans: closed population models, which assume no immigration, emigration, births, or deaths during the study period, and open population models, which allow for these changes in population size (Hammond, 1986; Otis, Burnham, White, & Anderson, 1978; Schwarz & Seber, 1999; White, Anderson, Burnham, & Otis, 1982). All previous studies on bottlenose dolphins in SZ have assumed closed populations (Öhman, 2010; Stensland et al., 2006) due to high level of resightings, low sightings outside of SZ, and the previously discussed evidence of genetic separation from dolphins in NZ. Discovery curves, showing the number of new individuals encountered per survey, are commonly used to verify this assumption, as the curve reaching an asymptote indicates that new animals are not entering the population (Gómez-Salazar, Trujillo, & Whitehead, 2011b; Reisinger & Karczmarski, 2010; Stensland et al., 2006; Wilson et al., 1999).

Other assumptions of MR exist for both closed and open population models, and include that marks are unique and that they are not lost over time (Elwen et al., 2009; Gómez-Salazar et al., 2011b; Hammond, 1986; Urian et al., 2015; Wilson et al., 1999). To ensure these assumptions are met using photo-identification data, an appropriate area of the animal must be targeted for photography, as discussed in section 1.4. Further assumptions of MR are related to the probability of capture; that the future catchability and survival of an individual is not affected by the previous marking of that individual (Gómez-Salazar et al., 2011b; Hammond, 1986; Urian et al., 2015; Wilson et al., 1999). This can be a major concern in MR studies done by physically capturing and marking the individuals; however, with photo-identification, the lack of physical interaction between observer and animals makes the likelihood of affecting an individual's survivability and future catchability negligible (Gómez-Salazar et al., 2011b; Wilson et al., 1999).

The final assumption for MR studies is the heterogeneity of capture probability; that the likelihood of capturing any one individual is the same as for any other individual (Hammond, 1986; Pollock, 1982; White et al., 1982). Due to different behaviours amongst individuals, including differences in the use of the study area, and attraction or avoidance of boats (e.g. by mother-calf pairs (Elwen et al., 2009)), this assumption is rarely met (Elwen et al., 2009; Hammond, 1986; Reisinger & Karczmarski, 2010; Wilson et al., 1999). Violating this assumption results in an under-estimation of true abundance (Hammond, 1986). The effect of violating the assumption of heterogeneity of capture probability on model results can be reduced by maximizing capture probability (e.g. increased field effort, pooling data, complete coverage of groups during photography) (Elwen et al., 2009; Reisinger & Karczmarski, 2010; Wilson et al., 1999). It can also be accounted for, to some extent, by using the closed population mixture models developed by Pledger (2000) during analysis.

1.5 Acoustic Analysis of Dolphin Whistles

Amongst bottlenose dolphin acoustics, much of the research has focused on *T. truncatus* (Buckstaff, 2004; Cook, Sayigh, Blum, & Wells, 2004; Wang et al., 1995b). However, because of their similar repertoire and usage, as well as unclear taxonomy (see above), these studies provide useful background information for studies of *T. aduncus* as well (Gridley, 2010; Gridley et al., 2012; Hawkins, 2010; Morisaka et al., 2005b).

Vocalizations of bottlenose dolphins have been broadly categorized into two separate classes: broad-band pulse signals and narrow-band, frequency-modulated whistles (Cook et al., 2004; McCowan & Reiss, 1995; Morisaka et al., 2005b; Schultz, Cato, Corkeron, & Bryden, 1995). A third type of sound is also produced by dolphins, although rarely, and are called low-frequency, narrow-band sounds (Simard et al., 2011). Pulse signals are further classified into echolocation clicks and burst-pulses (Cook et al., 2004; Schultz et al., 1995; Simard et al., 2011) and, along with low-frequency, narrow-band sounds, are not applicable to this study. Bottlenose dolphin whistles are tonal sounds with frequencies generally between 4-20 kHz (Schultz et al., 1995), although extremes of 0.8 kHz and 28.5 kHz have been reported (see review in Simard et al., 2011). Whistles are used in a variety of social interactions, including group cohesion, individual identification, the communication of information between individuals, and during feeding activities (see review in Hawkins, 2010; Janik, 2009; May-Collado & Wartzok, 2008), and are the focus of the acoustic component of this study.

1.5.1 Dolphin Whistles

Signature whistles account for roughly half of the total whistles an individual emits in the wild (Cook et al., 2004; Gridley et al., 2012; Janik, King, Sayigh, & Wells, 2013), and are characterized by a unique frequency modulation pattern, which is learned early in life and generally stays constant throughout (Janik et al., 2013). These whistles broadcast the identity of an individual, based on these distinct patterns, and are also used for group cohesion by helping to locate and maintain contact with other individuals (Cook et al., 2004; Janik & Slater, 1998). Little is known about the uses of other whistle types, often termed "variant" whistles, but Cook et al. (2004) found the production rate of variant whistles increased when animals were socializing as opposed to other activities, suggesting a social component. Janik et al. (2013) found many variant whistles during encounters that included calves. They suggest that variant whistles may be part of the process through which an individual obtains its unique signature whistle as it matures.

Most research on dolphin whistles focuses on signature whistles, which are largely learned (Janik, 2013; Janik et al., 2013), but also adapt to environmental factors (Buckstaff, 2004). Sufficient evidence has been found that signature whistles are not determined genetically (Fripp et al., 2005), and are learned through conspecifics (Fripp et al., 2005; Janik, 2013; Janik & Sayigh, 2013). It

appears as though individuals learn their signature whistles by selecting another individual's whistle, or sound from the environment, and modifying it enough to be considered unique (Janik, 2013). The whistle chosen is often from an individual that is not closely related and who rarely associates with the calf or mother (Fripp et al., 2005). These whistles then remain largely unchanged for life; although some males, when forming alliances with other males, do change their whistles slightly to more closely resemble their allies (Janik & Sayigh, 2013). Although signature whistles are learned, environmental noise can influence the production rate and certain acoustic parameters, such as frequency shifts and duration, of all whistle types (Buckstaff, 2004; May-Collado & Wartzok, 2008).

1.5.2 Whistle Variation Amongst Cetaceans

Early studies involving cetacean vocalizations primarily looked at inter-specific variation amongst whistles to determine what, if any, parameters differed between species (Oswald, Barlow, & Norris, 2003; Rendell, Matthews, Gill, Gordon, & Macdonald, 1999; Steiner, 1981; Wang, Würsig, & Evans, 1995a). Studies of five dolphin (Steiner, 1981), and seven (Wang et al., 1995a) and nine odontocete (Oswald et al., 2003) species determined that inter-specific whistles differed from each other in terms of duration and number of both inflection points and steps. Frequency parameters had low variability in all three studies. Rendell et al. (1999) studied five odontocete species and also found inter-specific variation amongst whistles, but mostly in the mean call frequency.

Quantitative analysis of intra-specific whistle variation, based on groups or populations, have also been performed on cetacean species (Ansmann, Goold, Evans, Simmonds, & Keith, 2007; Gridley et al., 2012; Hawkins, 2010; May-Collado & Wartzok, 2008; Morisaka et al., 2005b; Rendell et al., 1999). On a macrogeographic scale, and depending on the species in question, Rendell et al. (1999) determined that variability in intra-specific whistles was based on maximum frequency, number of inflection points, frequency range, or duration. In short-beaked common dolphins (*Delphinus delphis)* around the British Isles, variation amongst two groups was found in most frequency parameters (start, end, minimum, maximum, mean, absolute gradient, and range), as well as number of inflections (Ansmann et al., 2007). Differences in the whistles of *T. truncatus* populations have also been studied on a microgeographic level. Wang et al. (1995b) found low variation for all frequency parameters, whereas May-Collado and Wartzok (2008) found greatest variance in maximum frequency, end frequency, frequency range, and number of harmonics.

Studies have also been performed on different populations of the study species, *T. aduncus*, and found whistle parameters to also vary between populations on both the macro and microgeographic scales (Gridley et al., 2012; Hawkins, 2010; Morisaka et al., 2005b). Hawkins (2010) and Morisaka et al. (2005b) found maximum frequencies, number of inflection points, and harmonics to differ amongst populations. End frequency (Morisaka et al., 2005b), duration, and minimum frequency (Hawkins, 2010) were also variable. Gridley et al., (2012) studied bottlenose dolphins in the same locations as

this study, but combined the data from NZ and SZ into one group. When comparing the Zanzibar signature whistles to those of the other study area, Plettenberg Bay, South Africa (PB), they found that whistles from the two regions differed most in their end and maximum frequencies, but also amongst their absolute frequency gradients, change in frequency, duration, and number of inflection points. In the adopted frequencies, a measure of frequency range (see section 2.3.2), no major differences were found at the 5 kHz band level, but were found in both the 10 and 15 kHz bands (Gridley et al., 2012).

1.6 Aims and Objectives

This study aims to investigate potential linkage between bottlenose dolphins from NZ and SZ, and provide an updated estimate of dolphin abundance for these two areas. Population linkage will be investigated using photo-identification data, collected during two sequential field periods in SZ and NZ, and by examining variation amongst whistle characteristics from dolphins recorded in NZ, SZ, and another population, PB. If deemed appropriate by these investigations, an estimate of abundance for the entire island (ZB) will also be generated.

2. Materials and Methods

2.1 Study Area

Data collection took place at three different sites around southern Africa: two around Zanzibar Island (ZB), Tanzania and one in Plettenberg Bay (PB), South Africa (Figure 2).

In Zanzibar, surveys were conducted from the north coast (NZ, -5.768^{0}S, 39.354^{0}E), departing from Nungwi, and the south coast (SZ, -6.441^{0}S, 39.457^{0}E), departing from Kizimkazi. North Zanzibar (NZ, study area of roughly 110 km^2) and south Zanzibar (SZ, study area of roughly 89 km^2) are separated by only 80 km (Gridley, 2010). North and south Zanzibar have similar habitat characteristics, and the bottom is composed of seagrass beds, sandy bottoms, coral patches, and coral reef (Gridley, 2010). Both NZ and SZ are comprised of open spaces, with no bays or lagoons, but both study areas include islands.

Plettenberg Bay (-34.018^{0}S, 23.419^{0}E), located 3000 km from Zanzibar, is a half-heart shaped bay with four estuaries, a gradual depth gradient, and protection from prevailing swell (Smith, 2005). The PB coast is characterized mainly by exposed rocky headlands and fine sandy beaches (Jackson & Lipschitz, 1984). There are four estuarine environments within PB, and also small areas of wave-cut rocky platforms (Jackson & Lipschitz, 1984). Depths in the bay do not generally exceed 50 m, and there is a 1.5-2 m tidal range (Penry, Cockcroft, & Hammond, 2011). Plettenberg Bay was chosen as a third study site because genetic data indicate shared haploytpes between PB and Zanzibar dolphins (Gridley, 2010).

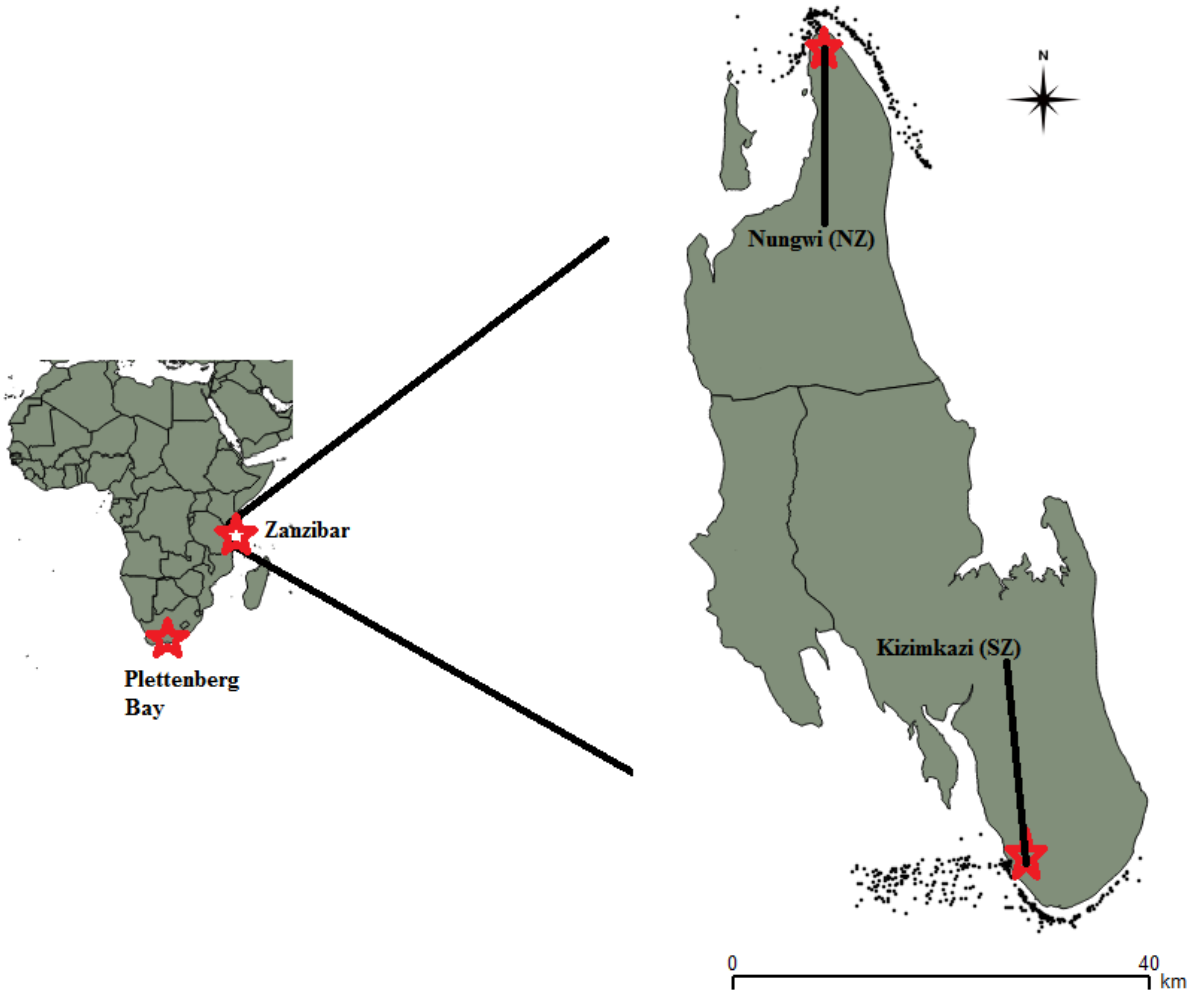

Figure 2: Map of north Zanzibar (NZ) and south Zanzibar (SZ). Black dots represent GPS coordinates taken every 15 minutes while on cruise.

2.2 Data Collection

In ZB and PB, dedicated boat-based surveys were carried out by T. Gridley in good weather conditions (≤ 4 Beaufort Sea State), using flexible survey routes to locate dolphins. Both acoustic and photo-identification data were collected, with at least two observers present. Photographic identification data for PB was not available, or applicable, for use in this study. Surveys in Zanzibar occurred over the course of 33 non-consecutive days between January 25 and March 22, 2008. Between January 25 and February 22, 2008, surveys were conducted over 19 non-consecutive days in SZ. Subsequently, data collection shifted to NZ, and surveys occurred on 14 non-consecutive days from February 26 to March 22, 2008. Data from PB were collected over 10 non-consecutive study days in March 2009.

Flexible route boat-based surveys were conducted with the focus of finding dolphin groups, rather than covering the entire area each day, or following pre-set transects. This flexible survey design was

chosen in order to maximize the number of encounters and sightings, and was partially achieved through communication with other dolphin observers. Cheney et al. (2014) found that more a flexible design allows for the targeting of areas that are used more often by the dolphins, and therefore results in an increase in the number of encounters. This leads to a greater number of photographs (Cheney et al., 2014), and, consequently, allows for a reduction in the effects of violating the heterogeneity of capture probability assumption (Hammond, 1986). Additionally, a more flexible survey design is likely to produce a more accurate estimate of the proportion of well-marked animals, which is essential in obtaining an overall estimate of abundance, and to increase capture probabilities (Cheney et al., 2014). Flexible route surveys are also expected to lead to a sample that is larger, and more representative of the entire population (Cheney et al., 2014). Contrarily, stricter survey methods may not consider how populations use their range, and may introduce uncertainties in abundance estimates (Forney, 2000). Stricter survey methods may also compound the problems associated with heterogeneity of capture probability, resulting from temporal changes in distribution or ranging patterns (Cheney et al., 2014).

Each survey was undertaken specifically to locate dolphins, and groups were defined by having all visible individuals within 100 m of each other, and interacting together, or engaging in similar behaviour, as per Irvine, Scott, Wells, and Kaufmann (1981). Upon encountering a group, general information, such as group size estimates, presence or absence of calves, as well as group behaviour, including feeding, resting, socializing, milling, and travelling, were recorded. Whenever a new group joined a group already being studied, the time was recorded and new encounter information was collected. To minimize the effect of violating the heterogeneity of capture probability assumption for Mark-Recapture (MR) analysis, careful attempts were made to photograph all individuals in a group, with no preference given to marked vs unmarked individuals, as per Elwen et al. (2009) and Wilson et al. (1999).

In Zanzibar, all data were collected from a 5 m aluminum boat, powered by either a 40 or 80 hp outboard motor. To collect the acoustic data, a hydrophone, model HTI-96-MIN (Scorpion Oceanics, Essex, UK), was positioned 6 m below the surface whilst the boat was stationary. Data were recorded with an Edirol UA-25 sound to PC medium (Roland, Dolphin Music, UK) at a sampling rate of 96 kHz, with a flat frequency response between 2 Hz and 30 kHz (±1 dB). Photographs were taken with a Canon EOS 350D digital SLR (Canon, UK) camera, equipped with a 55-200 mm zoom lens. Position was recorded every 15 minutes using a Garmin eTrex handheld GPS (Garmin, UK). Acoustic data from PB were collected from a 6.3 m fiberglass boat with two 85 hp motors, using the same hydrophone and settings as in Zanzibar, deployed to a depth of 2 m from the boat. Part way through data collection in PB, the hydrophone was lost at sea and replaced with a Magrec HP/30 General Purpose (Vanishing Point Marine, Plymouth, UK), deployed at a depth of 2.5 m below the surface whilst the boat was stationary. Data were recorded using an Edirol R1 medium (Roland, Solid

State Sound, Dorset, UK) at a sampling rate of 44.1 kHz and a flat frequency response between 200 Hz and 15 kHz (±1.5 dB). Position data was noted for each encounter, using the same handheld GPS as in ZB.

2.3 Data Processing

2.3.1 Photographic Identification

A database was compiled using Microsoft Access 2010 (Microsoft® software) to record information on area, date, cruise number, and encounter number of each photograph, prior to analysing the photos. Each photo was viewed, using Picasa[3] (Google, Inc. 2015), to identify the number of dorsal fins in the photo, and which side of the animal had been photographed. Each fin in the frame was then numbered from left to right. Any relevant information regarding the pictures, or the fins, was noted and added to the database.

Urian et al. (2015) found that there can be a significant amount of variation in how individual researchers process photo-identification data, and suggest potential methods to mitigate this. Each dorsal fin image must meet certain criteria, regarding both the quality of the image and the distinctiveness of the fin, to be included in analysis (Urian et al., 1999). These criteria ensure that individual dolphins are identified correctly, that twinning is avoided, and that there is a high likelihood of being matched. Regarding grading the quality of an image, Urian et al. (2015) state that image clarity is the most important factor, with exposure, lighting, angle, and amount of the fin visible also worth considering. The specific system for grading image quality is not considered as important as clearly stating the methods used, and providing examples (Urian et al., 2015). Scoring distinctiveness is much more subjective, and what is considered distinct may vary based on population size, length of the study, and frequency of sampling periods (Urian et al., 2015). Many researchers require matches to be confirmed by an experienced researcher to reduce the number of errors (Urian et al., 2015).

With this in mind, image quality was assessed on a scale of 1-3, based on the system established by Wilson et al. (1999), with only images of quality 3 considered to be of sufficient quality for use in analysis. Any image of a fin that was found to be too small (height < 25 mm when image size was set to 40%) was given a rating of 1. This same rating was given to images of fins that were out of focus. A rating of 2 was given to images of fins that were obstructed, partially obstructed, or not more or less perpendicular to the camera. The images of all remaining fins were given a rating of 3, are referred to hereafter as "good quality," and were used in analysis. To aid in obtaining the best quality image of each individual fin, all fins in good quality images were further rated based on their level of lighting. A rating of 3.1 was given to fins in images with dull colours, 3.2 for any image in which the fin was backlit, and images of well-lit fins were given a rating of 3.3.

Distinctiveness of each fin was graded on a scale of 1-5, following Elwen et al. (1999) (see Table 1 for descriptions of each grade). Grading was based on long-lasting marks, such as nicks or notches, abnormally shaped fins, deformities, large scratches, and white fin-fringes, which are considered permanent (Urian et al., 2015; Wilson et al., 1999; Würsig & Jefferson, 1990; Würsig & Würsig, 1977). To allow for re-identification of individuals, both during this study, and over time, only animals with a distinctiveness rating ≥ 3 were considered to be sufficiently unique for use in MR analysis. These fins had sufficiently long-lasting marks and are hereafter referred to as "well marked" individuals. This was to ensure the MR assumptions of marks being unique and not lost were not violated. Marks such as subtle scratches or skin disorders were not used as a means of primary identification because they can heal and disappear over time (Urian et al., 2015); however, given that the data were collected over a short time span (< 2 months), they were used, in some cases, as secondary markings to confirm matches because these markings likely last for a few months (Würsig & Jefferson, 1990). Although marks can change over time, given the relatively short time period during which the data were collected, this is not a concern in this study (Elwen et al., 2009). Figure 3 provides examples of fins from the three usable distinctiveness levels and photo quality ratings.

Table 1: Distinctiveness ratings, and their descriptions, for use in Mark-Recapture analysis (Elwen et al., 2009).

Rating	Description
1	No mark
2	Small, single mark or no marks and some scarring
3	1 large mark/nick or > 1 small mark, scarring, unusual fin shape
4	> 2 clear marks, the animal is easily identifiable
5	Very obvious marks, fin can be identified even with a low quality photo

Figure 3: From left to right examples of fin distinctiveness scores 3, 4, and 5, and photo quality ratings 3.3, 3.1, and 3.2. Orange circles show scratches, yellow arrows show small nicks, and red arrows show big notches. Photos taken in NZ by T. Gridley (2008).

The natural markings of the animals were the basis of the identification process, and each dorsal fin was visually inspected to assess these markings. Based on the markings on the dorsal fin, individuals were given a unique ID number. A catalogue of identified dolphins, comprised of the best quality images of each identified individual's dorsal fin, from both the left and right sides if possible, was then compiled. Each fin was subsequently compared to the catalogue and, if found to match an individual in the catalogue, labelled accordingly. If a fin was not found to match any of the individuals in the catalogue, and was identifiable by its unique markings, it was given an ID number and added to the catalogue. As subsequent pictures of a previously identified individual were found, the catalogue was updated to include only the best quality images of the individual from each side. Upon completion of data analysis, all matches of individuals in photos of quality ≥ 2, including individuals of all distinctiveness scores, were checked and verified by an external researcher with photo-identification experience. Calves, whether marked or unmarked, were not included in analysis, as their probability of capture is not independent of their mother (Stensland et al., 2006; Wilson et al., 1999), and were recognized by a close association with their mother (Wells & Scott, 1990).

2.3.2 Whistle Extraction

Whistle contours, defined as the modulation pattern of the fundamental frequency (Gridley et al., 2012), were identified visually from Adobe Audition 2.0 (Adobe Systems Incorporated), using a Hanning window and 512 fast Fourier transform (FFT) resolution. Frequency measurements at 5 ms intervals were then extracted for use in prior studies (Gridley, 2010; Gridley et al., 2012). Examples of whistles are given in Figure 4. In order to separate whistles from other vocalizations, only contours where part of the fundamental frequency was above 3 kHz, and only whistles longer than 0.1 s were considered (Gridley et al., 2012). Only the fundamental frequency, no other harmonic, was indexed, and contours separated by very short (< 0.03 s) breaks were considered one whistle (Gridley, 2010; Gridley et al., 2012). Each whistle was measured for its start and end time, if possible, and "visually assessed and graded based on the signal-to-noise ratio (1: signal is faint and barely visible on the spectrogram, 2: signal is clear and unambiguous, 3: signal is prominent and dominates)" (Gridley et al., 2012). Only those whistles with a clear start and end time, a clear overall shape, and a signal-to-noise ratio grade ≥ 2 were considered extractable and usable for this study. Whistle contours were traced using a custom written program in MATLAB v 6.5.1 (The Math Works, Inc.) called "Beluga" (Deecke & Janik, 2011). This program extracted the fundamental frequency, with manual corrections being applied as needed (display settings: FFT size 2048, 512 frame length, 87.5% overlap, and a Hanning window).

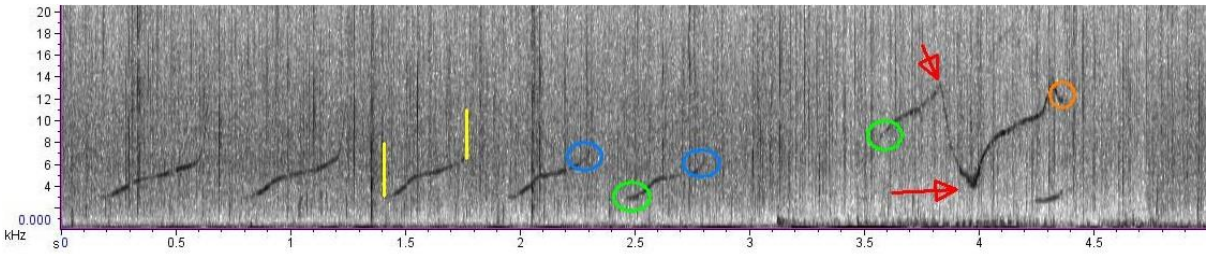

Figure 4: Examples of extracted whistles from NZ, recorded in 2008, and displayed in Raven Pro 1.5 Beta Version (The Cornell Lab of Ornithology, 2013) using a Hanning window and 512 FFT resolution. Vertical yellow lines represent the start and end of a whistle, red arrows point to inflection points, green circles show positive beginning slope, blue circles show positive end slope, and the orange circle shows a negative end slope.

The whistle contour data were then processed with a purpose written MATLAB 6.5.1 (The Math Works, Inc.) script (Gridley, 2010) to automatically measure 25 different parameters. Sixteen of these were chosen, along with the adopted frequency in the 5, 10, and 15 kHz bins (AF5, AF10, and AF15) (Gridley, 2010; Gridley et al., 2012; May-Collado & Wartzok, 2008; Morisaka, Shinohara, Nakahara, & Akamatsu, 2005a), for a total of 19 parameters used in this study. Adopted frequency is an arguably more effective measurement of frequency range than the simple calculation in Table 2, and is calculated by counting the number of data points (5 ms time intervals) that fall into 1 kHz frequency bins. These are then normalized for whistle duration to give a proportion of the whistle that fits into each bin. The 16 automatically measured variables used in this study include standard parameters such as start frequency, end frequency, maximum frequency, minimum frequency, frequency range, duration, beginning slope, end slope, and number of inflection points, as well as the mean frequency, frequency change, frequency at the first, second, and third quartiles, frequency gradient, and number of steps. These variables were chosen to match the variables used in other studies of bottlenose dolphin whistles (Ansmann et al., 2007; Díaz López, 2011; Gridley et al., 2012; May-Collado & Wartzok, 2008; Morisaka et al., 2005b; Oswald et al., 2003; Rendell et al., 1999; Wang et al., 1995a). Descriptions of these 16 variables, as well as the abbreviations that will be used hereafter to describe them, are given in Table 2.

Table 2: Acoustic parameters automatically measured from extracted whistles, along with their abbreviations, and a brief description of each parameter.

Parameter	Abbrev.	Description
Start Frequency	SF	Frequency at beginning of contour (kHz)
End Frequency	EF	Frequency at end of contour (kHz)
Maximum Frequency	MAXF	Highest frequency value in the contour (kHz)
Minimum Frequency	MINF	Lowest frequency value in the contour (kHz)
Frequency Range	FR	Maximum frequency – minimum frequency (kHz)
Frequency Change	CF	End frequency – Start frequency (kHz)
Mean Frequency	MEANF	Average frequency of each contour (kHz)
1st Quartile Frequency	1QF	Frequency at the 25% time duration (kHz)
2nd Quartile Frequency	2QF	Frequency at half time duration (kHz)
3rd Quartile Frequency	3QF	Frequency at 75% time duration (kHz)
Frequency Gradient	FG	(End frequency-Start frequency)/Duration (kHz/s)
Duration	DUR	Length of time of each contour (s)
Beginning Slope	BSL	Whether the slope of the whistle contour (change in frequency over time) is positive (1), negative (-1) or constant (0) at the beginning of the contour
End Slope	ESL	Whether the slope of the whistle contour (change in frequency over time) is positive (1), negative (-1) or constant (0) at the end of the contour
Inflection Points	INF	A count of the number of times the contour slope changes from positive to negative or vice-versa. Uses a moving average of 5 data points
Steps	STEP	A count of the number of times the contour has a constant frequency followed by a steep frequency, followed again by a constant frequency using a moving average of 5 data points

2.4 Statistical Analysis

2.4.1 Population Estimates

Capture histories were compiled for each identified individual, after selecting only good quality photographs of well marked animals, for both the northern (NZ) and southern (SZ) study sites, and both combined (ZB). Days were selected as sampling occasions, rather than encounters, as is common with studies of this nature (Elwen et al., 2009; Öhman, 2010; Stensland et al., 2006; Wilson et al., 1999). To investigate population closure, discovery curves were created by plotting the

cumulative number of newly identified individuals against the number of study days (Gómez-Salazar, et al., 2011b; Reisinger & Karczmarski, 2010; Stensland et al., 2006; Wilson et al., 1999). To investigate residency, sightings frequencies, the number of days that each individual was identified, were also plotted (Stensland et al., 2006). Both the discovery curves and sightings frequencies were created for SZ, NZ, and ZB, using Microsoft Excel 2010 (Microsoft® software).

Mark-recapture analyses were run in Programme Mark using the RMark interface (Laake, 2013) in the Tinn-R environment (Tinn-R Editor Version 2.4.1.5 2013). Both closed and open population models were run for each area. Closed population models were run to allow for comparison with earlier studies in the area, which also used closed population models (Stensland et al., 2006; Öhman, 2010). However, the death of an identified individual in SZ during the sampling period, as well as the results of this study, which show movement from SZ into NZ during the study period, violate the assumption of a closed population (Hammond, 1986; Otis et al., 1978; Schwarz & Seber, 1999; White et al., 1982). Therefore, open population models were considered to be a more accurate representation of the dolphin population around the island. For both model types, constant parameters are represented by (.), time dependent by (t), and equal to the preceding parameter by (). Parameters of closed population models may also include a mixture to partition the animals into separate groups with similar capture probabilities (Pledger, 2000), and are represented by (m).

2.4.1.1 Closed Population Mark-Recapture Models

When assuming a closed population, two types of model sets were considered: closed capture models (Otis et al., 1978), and Huggins closed capture models (Huggins, 1989). The most important difference between the two model sets, and the reason they are not comparable using the standard Akaike's Information Criterion (AIC) selection technique, is that the closed capture models include an additional parameter (an estimate of the number of animals in the population that were never detected) that the Huggins closed capture models do not. Huggins closed capture models are conditioned only on the number of individuals detected (Lukacs, 2010). Huggins closed capture models have an advantage over closed capture models because they allow for the inclusion of individual covariates to model the probability of an individual being captured, and the probability of recapturing an individual, provided it has been captured before (Lukacs, 2010). The Huggins closed capture models were therefore chosen for use in this study.

Huggins closed capture models were run using the calculation methods described by Lukacs (2010), based on the techniques described in (Huggins, 1989), and the mixture models from Pledger (2000) (models 3 and 4, below). Four models were run in the model set: 1) null model, 2) time varying model, 3) a model with an estimate of the effects of the heterogeneity of capture, and 4) a time varying model that also includes an estimate of the effects of the heterogeneity of capture. Capture heterogeneity is represented by parameter π, which is used to denote whether an animal has a high or

low capture probability based on that animal's capture history (Lukacs, 2010). Other estimated parameters in these models include the probability of being captured (p), and the probability of recapture, provided the individual has been captured before (c) (Huggins, 1991; White, 2008). Akaike's Information Criterion (AICc, corrected for small samples) was used to determine the best fitting model within each model set, as the lowest AICc value corresponds with the best fitting model (Huggins, 1991). For the ZB data, a covariate was introduced in the models to differentiate between capture occasions at NZ and SZ, and to take resightings of individuals in both areas into account.

2.4.1.2 Open Population Mark-Recapture Models

Before running the open population models, RELEASE goodness of fit (GoF) tests were performed to obtain the variance inflation factor ($\hat{c}$), which measures the lack of fit between the models. The variance inflation factor is calculated, as per Anderson, Burnham, and White (1994), using degrees of freedom (df) and the chi-squared statistic (x^2), as:

$$\hat{c} = \frac{x^2}{df}.$$

This gives an indication of whether the data are a perfect match to a fully time dependent Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) and, if not, how much they violate the assumptions. As $\hat{c}$ is unlikely to be a perfect fit (= 1), AICc will be replaced by a quasi-likelihood adjusted AICc (QAICc), which can be used for model selection (Anderson et al., 1994). For the GoF test, two tests were conducted: Test 2 and Test 3, with Test 3 having multiple components. Test 2 is a test of whether the assumption of equal capture probability holds true, and Test 3 tests the survivability assumption. Tests 3.SR and 3.Sm are related to survivability, based on subsequent resightings between capture occasions, relative to when they were first marked (Cooch & White, 2010). Tests 3.SR and 3.Sm combine to form the overall Test 3 result. This is then used with Test 2 to get the overall values for Test 2 + Test 3. The model is said to fit the data sufficiently if the value of $\hat{c}$ is < 4 (Anderson et al., 1994).

Open population models used in this study are those described by Schwarz and Arnason (2010), and follow the POPAN parameterization (Schwarz & Arnason, 1996) of the Jolly-Seber (JS) structure (Jolly, 1965; Seber, 1965). Estimated parameters included in these models are the probability that an individual will survive between two sampling occasions (Φ), the probability of capture at a given occasion (p), the probability of an animal entering the study area between sampling occasions (b), and the super population (N), an estimate of the total number of individuals, both captured and uncaptured, using the study area during the study period (Crosbie & Manly, 1985; Reisinger & Karczmarski, 2010; Schwarz and Arnason, 1996, 2010).

2.4.1.3 Calculating Total Abundance

Mark-recapture models only estimate the number of well marked individuals in the population ($\widehat{N}$), and not the total population (N) (Cooch & White, 2010; Lukacs, 2010; Schwarz and Arnason, 2010). Total abundance was calculated by extrapolating $\widehat{N}$ upwards, using the estimated proportion of well marked animals in the population (θ), using the formula provided by Williams et al. (1993) and Wilson et al. (1999) as:

$$N = \frac{\widehat{N}}{\theta}.$$

The estimated proportion of well marked animals (θ) in the population was calculated by obtaining the ratio of photos containing well marked individuals in good quality photos ($\hat{n}$), to photos of all individuals in good quality photos (n) (Williams et al., 1993; Wilson et al., 1999) using the formula:

$$\theta = \frac{\hat{n}}{n}.$$

A θ-value was calculated for each survey day, and the final θ-value for each study area was obtained by averaging the results of the daily θ-values. Coefficients of variation (CV) for both $\widehat{N}$ and θ (displayed as "x") were calculated as:

$$CV(x) = \frac{SE(x)}{x},$$

where SE is standard error. SE for $\widehat{N}$ was obtained from the model output, and for θ by:

$$SE(\theta) = \sqrt{\frac{\sum[(\theta' - \theta_t)^2]}{n}},$$

where θ' is the mean value of theta calculated daily, θ_t is the θ-value for a given day (t) and n is the number of survey days (Field, 2009). CV of N was then calculated using the CV of both $\widehat{N}$ and θ, as per Elwen et al. (1999), as:

$$CV(N) = \sqrt{(CV(\widehat{N}))^2 + (CV(\theta))^2}.$$

To avoid an unrealistic lower confidence limit, the log-normal confidence interval was calculated using:

$$r = \exp\left(1.96\sqrt{ln\left(1 + \left(CV(N)\right)^2\right)}\right),$$

as recommended by Burnham, Anderson, White, Brownie, and Pollock (1987). The lower and upper confidence limits were then calculated as N/r and N*r respectively, as per Elwen et al. (2009).

To further compare models, ΔAIC (the difference in the AIC value of each model from the AIC value of the best fitting model (the model with the lowest AIC value)) and Akaike weight were calculated (Burnham & Anderson, 2002). The term "AIC" is used here as a generic term to mean both AICc (used in the closed population models) and QAICc (used in the open population models) (Burnham & Anderson, 2002). Provided there are less than 100 models in the model set, models with a $\Delta AIC < 10$ may provide some level of support and should be examined further, and models with a $\Delta AIC < 2$ are considered of equal merit (Burnham & Anderson, 2002). If a model has an Akaike weight (w) of ≥ 0.9, then it is acceptable to infer that it is the correct model to use (Burnham & Anderson, 2002). However, if no model is clearly superior (all $w < 0.9$), Burnham and Anderson (2002) recommend computing a weighted average (wa) of all models, weighting them by their Akaike weights as:

$$wa = \sum_{i}^{R} w_i x_i.$$

In this case, x is the value being averaged, i is the model being averaged and R is the number of models in the set (Burnham & Anderson, 2002).

2.4.2 Acoustic Analysis of Whistles

2.4.2.1 Discriminant Function Analysis and Principal Component Analysis

Discriminant function analysis (DFA) is a multivariate method of analysing which parameters discriminate between individuals or groups through their means, and to what extent each variable explains the variation between them (McGregor et al., 2000; Sariyar-Akbulut, 2010; Terry, McGregor, & Peake, 2001). This is done by creating linear combinations of the measured variables and estimating how well a case, a whistle in this study, fits into its predefined group (McGregor et al., 2000). Discriminant function analysis has been successfully used to identify individuals of many different species through their vocalisations, including bald eagles (*Haliaeetus leucocephalus*) (Eakle, Mannan, & Grubb, 1989) and Queen Charlotte saw-whet owls (*Aegolius acadicus brooksi*) (Holschuh, 2004). Mitani et al. (1999) were also able to use DFA to correctly classify 78% of calls to the correct population of chimpanzees (*Pan troglodytes schweinfurthii*). More directly related to this study, DFA has been used successfully in detecting and explaining the variation in the whistles of different odontocete species (Oswald et al., 2003; Rendell et al., 1999; Steiner, 1981; Wang et al., 1995a). On an intra-specific scale, DFA has also been used to attempt to discriminate between whistles of neighbouring populations of *T. truncatus* (May-Collado & Wartzok 2008; Wang et al., 1995b). In these studies, Wang et al. (1995b) concluded that whistles differed significantly between

neighbouring populations, and May-Collado and Wartzok (2008) were able to correctly classify most of the individuals into their populations, concluding that the whistles of adjacent populations differed less than those separated by greater distances. For the study species, *T. aduncus*, Hawkins (2010) and Morisaka et al. (2005b) were able to use DFA to correctly classify whistles based on different populations. Duration, end frequency, maximum frequency, and harmonics were found to explain most of the variation amongst the populations (Hawkins, 2010; Morisaka et al., 2005b).

The crucial assumption for performing a DFA is that the means and variances must not be correlated (Jombart, Devillard, & Balloux, 2010). In this study, the assumption is likely to be violated, as some variables are calculated from others (i.e. CF = EF - SF). In order to satisfy this assumption, the data must be transformed, and a common method of transforming data for use in DFA is to first perform a principal component analysis (PCA) (Goodacre et al., 1998; Jombart et al., 2010; Sariyar-Akbulut, 2010; Timmins, Howell, Alsberg, Noble, & Goodacre, 1998). A PCA allows for a reduction in the dimensionality of multivariate data, while maintaining the variance (Goodacre et al., 1998; Timmins et al., 1998). This is done by finding patterns, through the use of standard deviation, covariance, Eigenvectors, and Eigenvalues, to transform the original variables into new ones, called principal components, by maximizing the variance in each successive component (Sariyar-Akbulut, 2010). These principal components are then assured to be uncorrelated and sufficient for use with, among other tests, DFA (Goodacre et al., 1998; Jacobs et al., 2013; Jombart et al., 2010; Sariyar-Akbulut, 2010; Timmins et al., 1998).

2.4.2.2 Analysis

To test whether or not whistles could be correctly classified into their respective areas (NZ, SZ, or PB) on the basis of acoustic parameters, a DFA was performed. All analyses on acoustic data were performed using STATISTICA 12 (StatSoft, 2013) 64-bit for Windows 7 (Windows® operating system). Prior to running the DFA, the data were first tested to ensure they satisfied the critical assumption of no correlation between the variable means and variances (Goodacre et al., 1998; Jombart et al., 2010; Sariyar-Akbulut, 2010; Timmins et al., 1998) using the correlation matrix function. As expected, due to the nature of the data (some variables were calculations from other variables), the resulting output indicated that the assumption was not met, as > 10 of the variables were correlated at the 0.05 significance level.

A PCA was therefore performed on the data to extract 18 independent and uncorrelated Factors to satisfy the assumptions for DFA, with area as the grouping variable. As correlation-based PCAs are more suitable for environmental data (Clarke & Warwick, 2001), such as exists for this study, a casewise analysis, based on correlations with variances calculated as SS/(N-1), was performed. Only those factors that satisfied Kaiser's criterion (Eigenvalue > 1) were used in the DFA (Kaiser, 1960). A casewise, stepwise DFA was then performed on the factor scores. A DFA extracts a certain number

of canonical roots, based on which number is smaller between the number of groups in the grouping variable minus one, and the number of variables in the analysis (Sariyar-Akbulut, 2010). As there are three areas (NZ, SZ, and PB), the DFA will result in two roots. Chi-square was used to determine whether the scores were significant at the 0.05 threshold (Oswald et al., 2003). The groupings for the DFA were defined *a priori,* based on geographic area. Each whistle was compared to the group centroids to evaluate how similar it was to each centroid. Based on that distance, each whistle was classified as belonging to one of the groups.

3. Results

In south Zanzibar (SZ), 23 cruises were conducted over the 19 survey days, resulting in 38 dolphin encounters. In north Zanzibar (NZ), 17 cruises were conducted over the 14 survey days, resulting in 26 encounters. There were 10 encounters during the 10 survey days in Plettenberg Bay (PB).

3.1 Photographic Identification

In SZ, 1837 photographs containing 3200 fin images were taken. Of these, 1327 fin images were of good quality. Three of the good quality fin images belonged to unmarked adults (distinctiveness score 1), and an additional 10 belonged to calves. There were a total of 113 individuals identified in SZ. Three of these individuals were identified only in low quality (image quality 2) photographs, and 15 identified individuals scored two for distinctiveness. These 18 animals were excluded from MR analysis, resulting in 95 well marked individuals in good quality photographs.

In NZ, a total of 2420 photographs were taken, resulting in 4247 dorsal fin images. Of these, 1685 fin images were considered to be of good quality. From these good quality fin images, 40 belonged to calves, 22 to unmarked adults, and a total of 127 individuals were identified. Ten of the identified individuals scored two for distinctiveness, and were therefore included with the unmarked adults for the purpose of statistical analysis. This resulted in a total of 117 well marked individuals in good quality photos in NZ.

For the two areas combined (ZB), 21 individuals were identified in both NZ and SZ. Two of these had distinctiveness scores of two, and three were found in good quality images in one area, but only in low quality photos (image quality 2) in the other. Therefore, a total of 16 well marked individuals in good quality photos were found in both NZ and SZ. A total of 219 individuals (113 in SZ + 127 in NZ – 21 in both) were identified in good quality photos in ZB. Twenty-three of these scored two on the distinctiveness scale and were included with the unmarked individuals, resulting in a total of 196 well marked individuals in good quality photos (95 in SZ + 117 in NZ – 16 in both). A summary of the data is given in Table 3, and examples of matches between NZ and SZ are provided in Figure 5.

Table 3: Summary of photo-identification findings, including date of collection and corresponding survey number, the number of good quality fins (all dolphins of photo quality > 2) photographed that day (Total Fins), the number of those fins identified as usable (adults of quality and distinctiveness > 2) individuals (Distinct Fins), the total number of individual dolphins of all quality and distinctiveness identified that day (Total ID), the number of unmarked adults photographed that day (Unmarked Fins), the number of usable (quality and distinctiveness > 2) individual animals identified that day (Usable ID), as well as the number of newly identified animals (New ID) for each region. Cumulative number of newly identified animals for ZB is separated in the far right column.

Date (2008)	Survey Number	Total Fins	Distinct Fins	Total ID	Unmarked Fins	Usable ID	New ID (SZ/NZ)	New ID (ZB)
South Zanzibar								
Jan. 25	1	3	3	2	0	2	2	2
Jan. 26	2	14	14	7	0	6	6	6
Jan. 29	3	17	17	10	0	10	10	10
Jan. 31	4	1	1	1	0	1	1	1
Feb. 1	5	62	61	25	0	21	10	10
Feb. 2	6	187	178	28	0	25	10	10
Feb. 5	7	184	157	41	1	33	17	17
Feb. 6	8	66	62	30	0	24	14	14
Feb. 7	9	39	36	22	0	19	1	1
Feb. 8	10	40	32	18	0	13	5	5
Feb. 10	11	33	32	30	0	20	4	4
Feb. 12	12	12	12	3	0	3	0	0
Feb. 13	13	55	53	20	0	18	0	0
Feb. 14	14	310	301	62	2	50	10	10
Feb. 15	15	83	80	33	0	29	4	4
Feb. 16	16	57	50	24	0	15	0	0
Feb. 17	17	26	26	4	0	4	0	0
Feb. 20	18	97	81	17	0	14	0	0
Feb. 22	19	31	31	5	0	5	1	1
	North Zanzibar							ZB (cont.)
Feb. 26	20	124	107	22	2	18	18	18
Feb. 28	21	175	168	51	2	45	38	37
Mar. 5	22	162	155	43	1	39	32	23
Mar. 6	23	53	51	19	1	17	4	4
Mar. 7	24	330	317	52	4	50	9	9
Mar. 11	25	134	131	27	1	27	1	1
Mar. 12	26	147	123	27	4	22	0	0
Mar. 14	27	90	90	40	0	37	5	5
Mar. 15	28	170	162	42	2	40	1	1
Mar. 16	29	30	24	7	1	6	0	0
Mar. 18	30	10	9	10	1	7	1	1
Mar. 20	31	20	20	7	0	7	0	0
Mar. 21	32	34	34	4	0	4	1	1
Mar. 22	33	166	161	47	3	43	7	1

Figure 5: Two of the 16 individuals found in both SZ (left side) and NZ (right side) in 2008. Photos: T. Gridley.

3.2 Discovery Curves

The discovery curves all seem to reach an asymptote (Figure 6). The number of times individuals were seen in each area was plotted in a frequency distribution plot (Figure 7). Resighting rates were generally high, at 62% for NZ, 76% for SZ, and 75% for ZB.

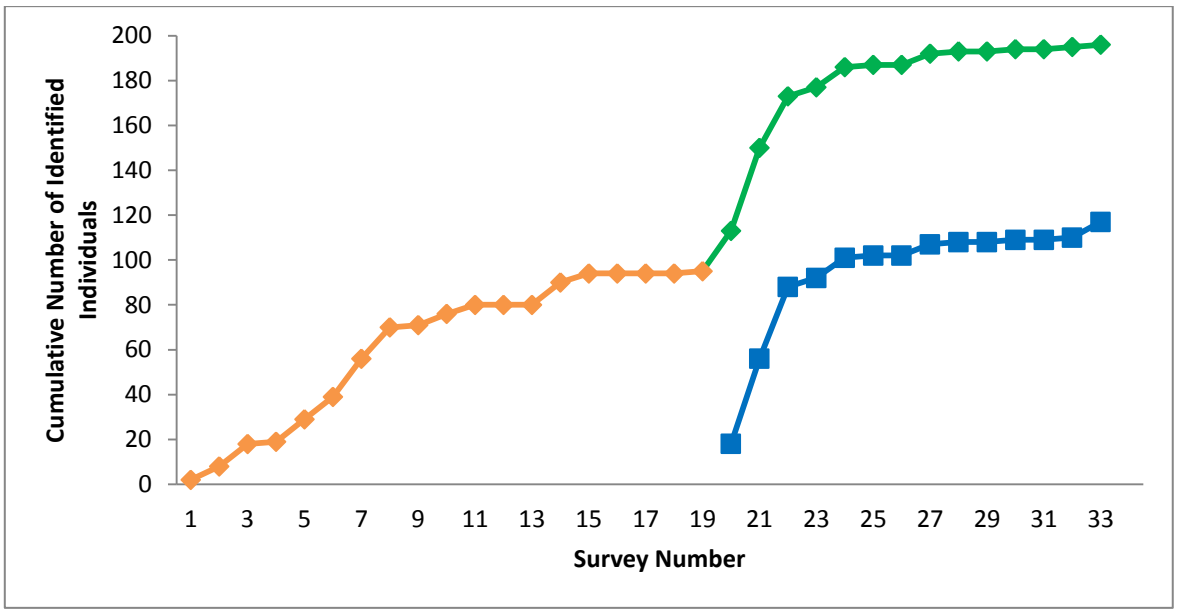

Figure 6: Discovery curves showing the cumulative number of identified bottlenose dolphins in SZ (orange diamonds) and NZ (blue squares) over the study period. Because all data from the first 19 days come from SZ, the discovery curve for ZB follows that of SZ for those 19 days and continues from the SZ curve in green diamonds.

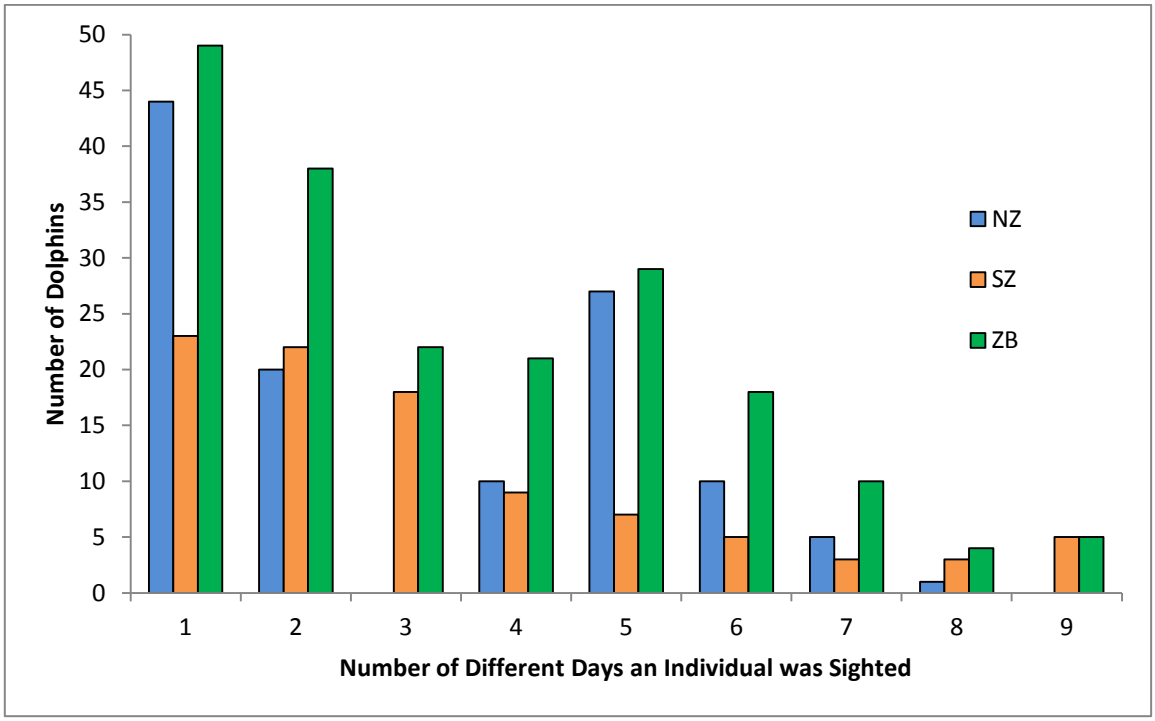

Figure 7: Frequency distributions showing the number of times individual dolphins were identified during the study period. NZ data is on the left in blue, SZ in the middle in orange, and ZB on the right side in green.

3.3 Abundance Estimates

The proportions of marked individuals in the populations (θ) were calculated as 0.94, 0.95, and 0.94 for NZ, SZ, and ZB respectively.

3.3.1 Closed Population Models

The best fitting models for all three data sets were those which varied over time, and included an estimate of the effects of the heterogeneity of capture (π(.)p(t+m)c()). No other model, in any of the data sets, had a ΔAICc < 10. Therefore, the numbers reported below (Table 4) all belong to the best fitting model. Complete model outputs are available in Appendix A.

Table 4: Results of the best fitting model (π(.)p(t+m)c()) of the Huggins closed population model sets, including Area and total population estimate (N), along with lower (LCL) and upper (UCL) limits at the 95% confidence level.

Area	N	LCL	UCL
North Zanzibar	203	149	275
South Zanzibar	109	95	126
Zanzibar Island	251	212	297

3.3.2 Open Population Models

RELEASE Goodness of Fit (GoF) tests resulted in variance inflation factor ($\hat{c}$) values of 3.27 (NZ), 2.84 (SZ), and 3.52 (ZB), which were all acceptably low (< 4). Full results of the GoF tests are presented in Appendix B. These $\hat{c}$ values were used to obtain QAICc values for each model, and these values were used to select the best fitting model for each data set. The time dependent model (Φ(t)p(t)b(t)N(.)) was the best fit for the ZB data, and no other model had a ΔQAICc < 10. For NZ, a partially time dependent model (Φ(t)p(t)b(.)N(.)) was found to be the best fit. A second model had a ΔQAICc of 6.4, but a weighted average was unnecessary because the best fitting model had an Akaike weight of 0.96, and was therefore deemed appropriate. In SZ, four models had a ΔQAICc < 10, and no model had an Akaike weight > 0.9. All models in the set were therefore averaged. Only the results from the best fitting models for NZ and ZB, as well as the weighted average of all models for SZ, are reported here (Table 5). Complete model results are available in Appendix C.

Table 5: Partial output of the open population POPAN models, including Area, total estimate (N) and lower (LCL) and upper (UCL) limits at the 95% confidence interval.

Area	N	LCL	UCL
North Zanzibar	149	128	173
South Zanzibar	120	97	149
Zanzibar Island	353	290	430

3.4 Whistle Analysis

A total of 1708 whistles were extracted from 06:31:50 (hh:mm:ss) of analysed recording time. The contours of 813 whistles were extracted from the 03:00:46 recorded in NZ, 384 from the 02:47:26 recorded in SZ, and 511 from the 00:43:38 recorded in PB. Box plots, showing the medians, upper and lower quartiles, and minimum and maximum values for the 19 acoustic variables, are shown in Figure 8a-e.

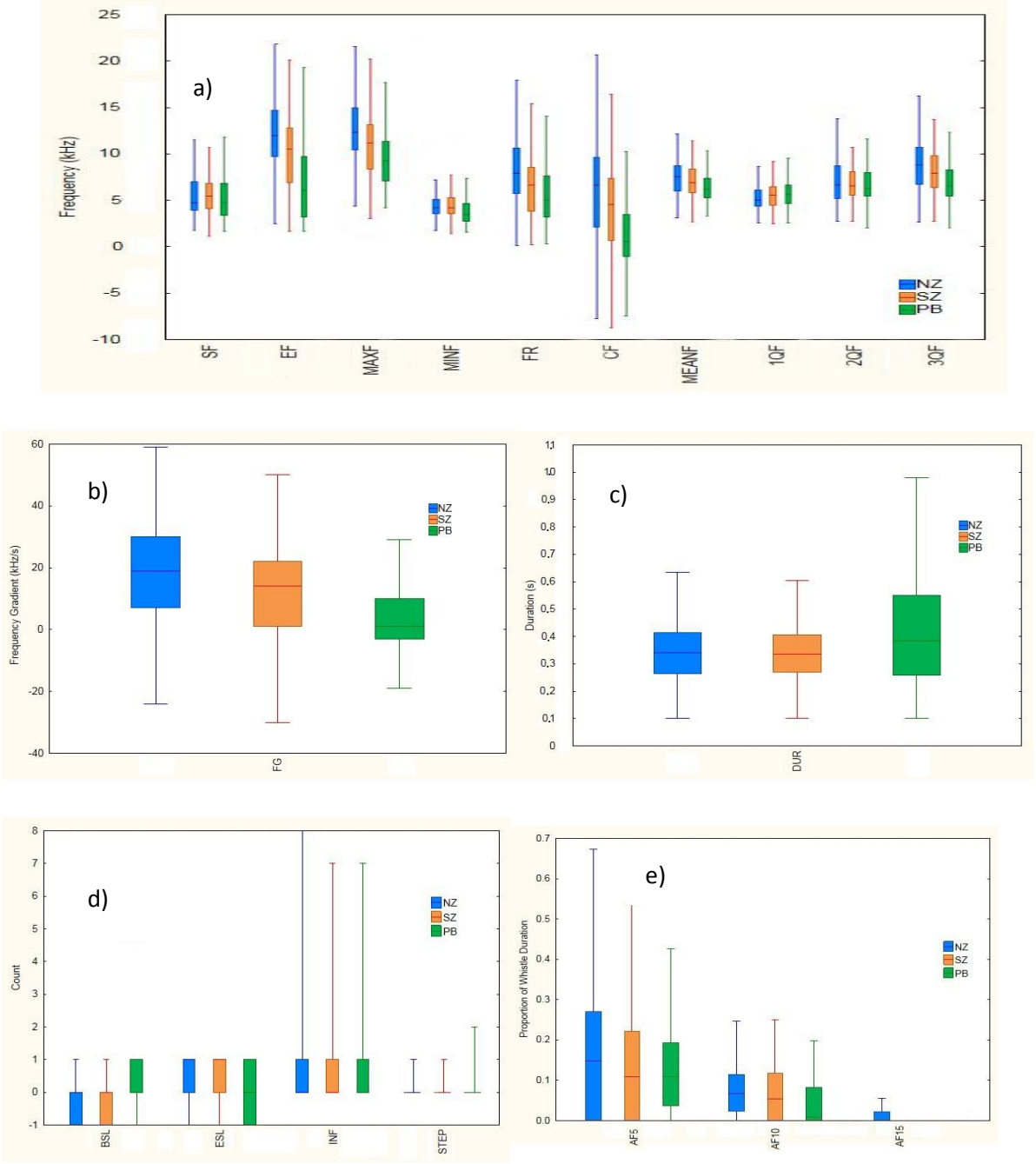

Figure 8a-e: Box plots showing the median, upper, and lower quartiles, and the minimum and maximum for all 19 acoustic parameters. For description of the parameters and abbreviations see Table 2. a: frequency parameters, b: frequency gradient, c: whistle duration, d: slope and count data, e: proportion of absolute frequency. In each graph, from left to right, the blue, orange and green boxes correspond to NZ, SZ, and PB.

3.4.1 Principal Component Analysis

Principal component analysis (PCA) resulted in five factors with Eigenvalues ≥ 1. Together, they explained 76.76% of the variance in the unpooled data set (NZ, SZ, and PB). The contribution of each acoustic variable (the proportion of variance attributed by each variable per factor), associated Eigenvalues, and percentage of the variance explained by each of these five factors are shown in Table 6. As evidenced by the variable contributions, Factors 1 and 2 are associated most strongly with whistle frequency parameters. Factor 1 includes end frequency, maximum frequency, frequency range, mean frequency, and frequency at both the midpoint and third quartile. Factor 2 is associated with start frequency, minimum frequency, change of frequency, frequency at the first quartile, frequency gradient, and the proportion of absolute frequency in the 5 kHz bin. Duration, end slope, and number of inflection points are associated with Factor 3. These three factors were found to load the highest on the two roots after the DFA was performed (Table 7).

Table 6: Variable contributions, the proportion of variance explained by each variable per factor, are shown in the upper portion of the Table. Below those: Eigenvalues, the % of variance each factor explains (%Variance) and the cumulative % of variance explained (%Cumulative) for each of the five factors are displayed.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
SF	0.01	**0.14**	0.06	0.12	0.00
EF	**0.13**	0.02	0.02	0.02	0.01
MAXF	**0.13**	0.00	0.01	0.04	0.00
MINF	0.02	**0.12**	0.11	0.01	0.00
FR	**0.09**	0.03	0.05	0.06	0.00
CF	0.08	**0.11**	0.00	0.01	0.01
MEANF	**0.13**	0.04	0.00	0.01	0.00
1QF	0.01	**0.15**	0.02	0.04	0.02
2QF	**0.08**	0.04	0.02	0.06	0.02
3QF	**0.12**	0.00	0.00	0.01	0.00
FG	0.07	**0.11**	0.00	0.02	0.01
DUR	0.00	0.00	**0.27**	0.06	0.02
BSL	0.00	0.04	0.09	0.27	0.01
ESL	0.04	0.02	**0.13**	0.05	0.02
INF	0.00	0.04	**0.15**	0.13	0.00
STEP	0.00	0.00	0.05	0.01	0.34
AF5	0.01	**0.07**	0.00	0.03	0.03
AF10	0.02	0.05	0.00	0.04	0.24
AF15	0.06	0.00	0.02	0.00	0.27
Eigenvalues	6.01	3.67	2.14	1.76	1.01
%Variance	31.65	19.30	11.26	9.24	5.31
%Cumulative	31.65	50.95	62.21	71.45	76.76

3.4.2 Discriminant Function Analysis

The DFA yielded two roots on the five principal components (factors), which are referred to as Root 1 and Root 2. Root 1 was found to explain 97% of the variance in the data, and Root 2 the remaining 3%. Factors 1-3 were found to load highly on Root 1, with coefficient values of -0.82, 0.43, and 0.51 respectively. Factor 3 also loaded highly on Root 2, with a coefficient value of -0.78 (Table 7).

Classification success was high (86.2%) for NZ and moderate for PB (61.8%). However, SZ had 0% classification success. Of the whistles from SZ, 73% (281/384) were assigned to NZ and 27% (103/384) to PB (Table 8). Means of the canonical scores for the DFA are reported as (Root 1, Root 2) and were found to be (-0.538, -0.051) for NZ, (0.037, 0.186) for SZ, and (0.828, -0.059) for PB. These values, along with associated standard deviation, are displayed in Figure 9. A plot of Root 1 vs. Root 2, including all values, can be found in Appendix D, and shows similar distribution around the centroid for all three groups. Although most divergence between the three populations was along Root 1, with only SZ diverging slightly along Root 2, there was much overlap between all populations along both roots.

Table 7: Results of the DFA including coefficient values for each factor on each of the two Roots, Eigenvalues, cumulative % of variance explained, chi-square statistic, degrees of freedom, and p-values for each Root, as well as Wilks, F, and p-values for each of the Factors.

	Root 1	**Root 2**	**Wilks'**	**F(2, 1701)**	**p-value**
Factor 1	**-0.82**	-0.22	0.89	172.49	< 0.01
Factor 2	**0.43**	0.33	0.79	65.18	< 0.01
Factor 3	**0.51**	**-0.78**	0.77	43.13	< 0.01
Factor 4	0.29	0.13	0.75	18.51	< 0.01
Factor 5	0.04	0.43	0.74	1.95	0.14
Eigenvalue	0.34	0.01			
Cumulative %	0.97	1.00			
x^2	520.75	17.10			
df	10.00	4.00			
p-value	< 0.01	< 0.01			

Table 8: Classification success and the number of whistles from each observed groups that were assigned to each group by the DFA, as well as the percentage of each group that was correctly assigned.

Observed Group	**Assigned Group**			
	NZ	SZ	PB	% Correct
NZ (n=813)	701	1	111	86.2
SZ (n=384)	281	0	103	0.0
PB (n=511)	184	11	316	61.8

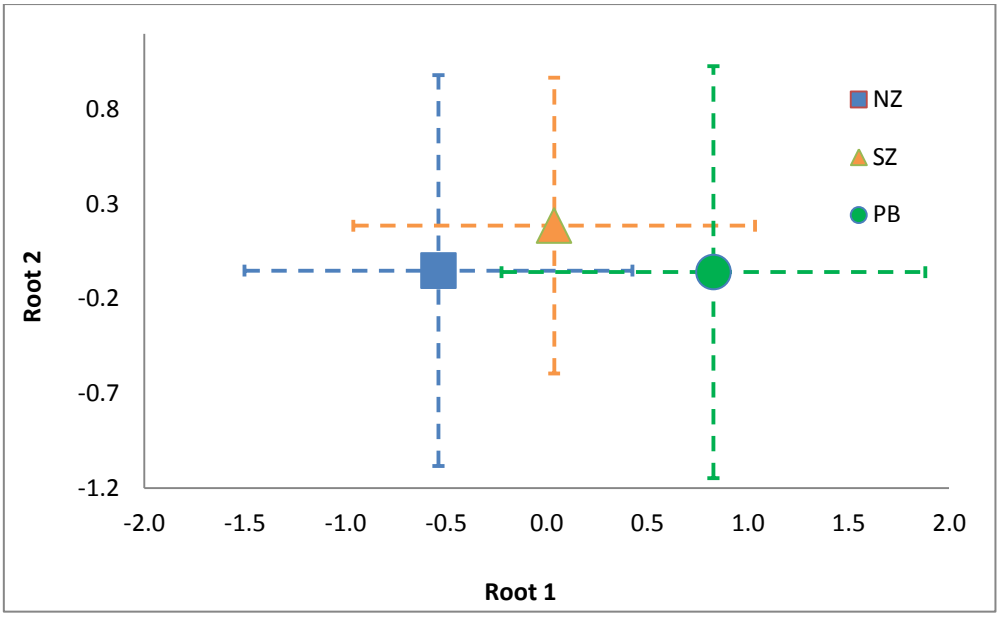

Figure 9: Plot of the means of the canonical scores for NZ (blue square), SZ (orange triangle), and PB (green circle), including standard deviation bars.

Results of the DFA show that whistles from NZ and PB differ in their frequency parameters. The most likely causes of this variation are change in frequency, frequency gradient, end frequency, maximum frequency, and frequency at the third quartile. SZ differs along these parameters as well, although much of the variation amongst its whistles is explained by duration, number of inflection points, and end slope. End slope and number of inflection points for SZ and NZ are quite similar, with PB showing a much higher number of inflection points, and fewer positive end slopes. The duration of whistles for SZ is in the middle of the other two populations. For all frequency parameters but minimum frequency, the biggest differences were between NZ and PB, with SZ fitting in the middle.

4. Discussion

This study used photographic and acoustic data to investigate population linkages between bottlenose dolphins off the north (NZ) and south (SZ) coasts of Zanzibar Island. The photographic data indicate connectivity between NZ and SZ, with 8.2% (16 of the 196 identified) of the animals observed in both study sites, despite the limited time frame of the study. Furthermore, whistles of bottlenose dolphins from SZ could not be distinguished from those of NZ or Plettenberg Bay (PB). Whistles of SZ dolphins were typically classified together with NZ whistles, indicating that whistles were shared between the two areas. Together, these findings indicate that bottlenose dolphins from SZ and NZ should not be considered as two separate, closed populations, but that bottlenose dolphins from around the coast of Zanzibar Island (ZB) should be considered as a single population unit, possibly with two resident female groups. Abundance estimates should be calculated accordingly.

When generating abundance estimates of SZ bottlenose dolphins from 2004 and 2007, Öhman (2010) used a study area of 270 km^2. Inside this area was a 26 km^2 area that had been used to generate abundance estimates from 1999-2002, which in turn contained a 1.7 km^2 area that included the highest concentration of dolphins (Stensland et al., 2006). Öhman (2010) also generated abundance estimates using only the same 26 km^2 area used by Stensland et al. (2006), and, for the sake of continuity, only the estimates derived using this 26 km^2 area will be discussed.

4.1 North and South Zanzibar

Both closed and open population models were used to generate 2008 population estimates for the bottlenose dolphins around both SZ and NZ. Closed population models were used to be consistent with all previous abundance estimates of dolphins from SZ (Öhman, 2010; Stensland et al., 2006). Berggren (2011) obtained an initial estimate of the NZ population; however, the methods used were not reported. Based on the conclusion that NZ and SZ be treated as separate populations, and that the data were collected over a short time frame (< 1 month), it is assumed that Berggren (2011) used closed population models. Results from both the photo-identification and the acoustic data show that when generating population estimates of NZ and SZ bottlenose dolphins separately, closed population models are inappropriate. Dolphins from the two areas should instead be treated as open populations, even over a short term study such as this.

This study found 16 well marked individuals in NZ after identifying them first in SZ, confirming the findings of Berggren (2011) and Öhman (2010) that animals move out of SZ and into NZ over short time periods. Additionally, one previously identified individual was killed as a result of bycatch during sampling in SZ. The emigration from SZ, immigration to NZ, and death in SZ are all clear violations of the closed population assumption required when using closed population models (Hammond, 1986; Otis et al., 1978; Schwarz & Seber, 1999; White et al., 1982).

Further evidence of the appropriateness of using open population models to generate estimates of abundance for bottlenose dolphins around SZ and NZ comes from the acoustic data. The DFA resulted in high classification success of whistles from NZ dolphins. Only 13.8% of NZ whistles were misclassified, suggesting that the acoustic structure of whistles from dolphins in NZ have unique characteristics that allow for correct classification. In contrast, the zero classification success for SZ dolphins (0/384 whistles classified correctly) suggests that whistles from SZ do not have a unique structure. A majority (73%) of these whistles were classified as coming from NZ. Given that whistles are learned (Janik, 2013; Janik et al., 2013), and that bottlenose dolphins mimic vocalizations of other individuals (Janik & Slater, 2000), the similarity of whistles between NZ and SZ animals suggests mixing between the two areas. This result supports the conclusion by Gridley (2010), which used a subsample of the data used in this study (only signature whistles) and found that there was

acoustic exchange and evidence of convergence on similar whistle form and features amongst bottlenose dolphins around Zanzibar Island.

Similar whistle forms amongst adjacent groups of bottlenose dolphins have also been found in other areas (Hawkins, 2010; May-Collado & Wartzok, 2008; Wang et al., 1995b). In each of these studies, the similarity of whistles was postulated to be the result of some degree of mixing between the two adjacent groups. Similar environments around NZ and SZ (Gridley, 2010) could have some impact on why whistles from SZ share characteristics with those from NZ, as whistle variation has been found to be influenced by environmental noise (Ansmann et al., 2007; May-Collado & Wartzok, 2008; Morisaka et al., 2005a). However, tourism intensity, and the resultant increase in boat traffic and noise, has been found to impact bottlenose dolphin whistle characteristics (Buckstaff, 2004; May-Collado & Wartzok, 2008). In Zanzibar, the high level of tourism in SZ (Christiansen et al., 2010; Stensland & Berggren, 2007) could influence the whistles characteristics enough to make them unique to those from NZ. As this has not happened, it provides further evidence that mixing is occurring between the two coasts. The results of the acoustic analysis support the findings of the photo-identification analysis of mixing between NZ and SZ, and therefore, that closed population models are inappropriate for generating abundance estimates of the bottlenose dolphins in NZ and SZ. Only the results using open population models are considered appropriate.

For NZ, a population estimate of 149 (95% CI 128-173) was obtained. This estimate is lower than the previous estimate of NZ dolphins (254 (95% CI 199-460)) (Berggren, 2011), and the CIs do not overlap, even though the same data were used in both studies. That the abundance estimate for NZ obtained by Berggren (2011) is higher than the estimate provided by this study is likely a direct result of the violation of the assumption of a closed population, as that tends to increase abundance estimates (Lindeman, 1990). Differing estimates could also be caused by variance in the rating of both distinctiveness and photo quality by different researchers (Urian et al., 2015). This cannot be confirmed however, as Berggren (2011) does not indicate how distinctiveness or photo quality were rated. The CIs of the population estimate obtained in this study using closed population models (203 (95% CI 149-275)) overlap with the CIs of both the estimate generated in this study using open population models, and with the estimate reported by Berggren (2011).

For SZ, the weighted average of the open population models resulted in an estimate of 120 (95% CI 97-149) bottlenose dolphins. This is the lowest estimate provided to date for the bottlenose dolphins around SZ, and the first for which the CIs do not overlap with all previous estimates, even though a higher estimate could have been expected for this study due to the larger study area (~89 km^2 vs. 26 km^2) (Öhman, 2010; Stensland et al., 2006). The CIs of the estimate provided in this study overlap with the all previously reported abundance estimates for SZ, other than 2001 (Öhman, 2010; Stensland et al., 2006) (Table 9). As with the estimate generated using open population models, the

estimate provided in this study using closed population models (109 (95% CI 95-126)) is also the lowest provided to date, and the first for which the CIs do not overlap with all previously reported estimates. This may suggest that the number of dolphins in SZ is declining; however, there is insufficient data to conclude whether this is a trend. Lower estimates may also relate to a lower number of encounters in this study, due to less observation days, compared to previous studies (Öhman, 2010; Stensland et al., 2006); however, this is unlikely to be the case as the resighting rate (76%) and estimated proportion of marked animals in the SZ population ($\theta = 0.95$) were both high for this study. The more likely reason for the lower estimate calculated in this study is the estimated 16 bycaught dolphins during the 2007/2008 season (Amir, 2010), as those animals were eliminated from the population.

Table 9: Population estimates (N) for bottlenose dolphins in south Zanzibar for each year, including lower (LCL) and upper (UCL) confidence limits at the 95% confidence level, number of survey days (Days), and references.

Year	N	LCL	UCL	Days	Reference
1999	150	142	172	11	Stensland et al. (2006)
2000	153	142	183	44	Stensland et al. (2006)
2001	179	167	212	45	Stensland et al. (2006)
2002	136	124	172	31	Stensland et al. (2006)
2004	163	92	233	31	Öhman (2010)
2007	139	124	182	40	Öhman (2010)
2008	120	97	149	19	This study

4.2 Zanzibar's Bottlenose Dolphins as One Population Unit

Analysis of both photo-identification data and whistle characteristics provide evidence of mixing between dolphins from the north and south coasts of Zanzibar Island; however, mixing between the two groups is not necessarily indicative of the need to consider the two groups as one population. Several studies of adjacent bottlenose dolphins groups around the world using photo-identification (Chilvers & Corkeron, 2003; Lusseau et al., 2006; Toth et al., 2012; Tyson et al., 2011), genetic (Parsons et al., 2006), and acoustic (May-Collado & Wartzok, 2008) analyses have concluded separate populations. In some of these cases, evidence of mixing between populations was also found, but they were still considered separate units (May-Collado & Wartzok, 2008; Toth et al., 2012; Tyson et al., 2011). Contrary to these, other studies have found it appropriate to consider adjacent groups as a single unit (Hawkins & Gartside, 2008; Krützen et al., 2004). As discussed below, the findings of this study support the treatment of dolphins from SZ and NZ as a single population unit.

Tyson et al. (2011) studied *T. truncatus* in Florida, USA using photo-identification, and concluded that dolphins from two adjacent areas should be considered as two distinct communities for

management purposes. This conclusion was the result of a low percentage (3.5%) of dolphins seen in both areas over the course of the four year study, and a large difference in the resighting rates of the two areas (45.7% vs. 28.3%) (Tyson et al., 2011). Similarly, Toth et al. (2012) concluded that *T. truncatus* around New Jersey, USA are separated into two distinct stocks based on photo-identification data that found differences between the two groups with respect to distance from shoreline, group size, occurrence of the barnacle *Xenobalanus globicipitis*, avoidance behaviour, and colouration. They also found only 4% of individuals in both regions during the six month study (Toth et al., 2012). A discrete community was also the conclusion of a photo-identification study of *T. aduncus* in Point Lookout, Australia (Chilvers & Corkeron, 2003). This conclusion was the result of finding no matches with this community and two adjacent groups (Chilvers & Corkeron, 2003). The number of well marked individuals identified in NZ after having been identified in SZ (16) increases to 19 when including well marked individuals that were seen in one area in good quality images, but only in images of quality 2 in the other. When comparing this to the 196 well marked dolphins that were identified in this study, 8.2-9.7% of all identified dolphins around ZB were sighted in NZ after being sighted in SZ during the two month study. When matched to earlier catalogues of the SZ population, Berggren (2011) found 25 dolphins in NZ in 2008 previously seen in SZ. This could potentially push the percentage of dolphins identified in both areas even higher, as more individuals were identified in both areas. The extent of the mixing in Zanzibar, as evidenced by the higher percentage of individuals identified in both SZ and NZ, is greater than in these others areas, and is evidence that mixing between the two putative populations occurs regularly. Furthermore, this higher percentage was found in spite of a much shorter sample period than in Florida (127 surveys) (Tyson et al., 2011), and a similar number of sampling days to the studies in Australia (33 days) (Chilvers & Corkeron, 2003) and New Jersey (29 surveys) (Toth et al., 2012). Additionally, the resighting rates of animals in NZ (62%) and SZ (76%) are both high, contrary to the difference found in Florida (Tyson et al., 2011). The lower resighting rate for NZ may largely be an artefact of low sampling effort, because six individuals previously identified in SZ were all identified in NZ on the last day of sampling.

A study involving common bottlenose dolphins in Costa Rica and Panama used DFA to investigate differences in the whistles of adjacent populations, and found 81.1% and 63.6% classification success for the two adjacent populations (May-Collado & Wartzok, 2008). Although dolphins from these two areas had moderate to high classification success, and in spite of the fact that no individual dolphins had been identified using both sites, it was postulated that the similarity in whistle parameters between dolphins from the two sites was the result of connectivity in the form of individuals moving between the areas (May-Collado & Wartzok, 2008). Given that SZ whistles could not be differentiated from NZ whistles, and that individuals were identified in both areas, the extent of the mixing may be greater amongst ZB dolphins than in the two populations in Panama and Costa Rica.

The results of the photo-identification analysis show that individuals travel the 80 km between NZ and SZ, and the results of the acoustic analysis suggest that there is significant influence between the two areas with respect to whistle characteristics. Together, this provides evidence for treating dolphins from the two areas as one population unit. Indo-Pacific bottlenose dolphins have been found to travel up to 600 km (Shirakihara, Shirakihara, Nishiyama, Iida, & Amano, 2012), so the distance between the areas is not a hindrance. However, the study by Särnblad et al. (2011), which found genetic differentiation between NZ and SZ bottlenose dolphins, cannot be ignored. Särnblad et al. (2011) found evidence of mitochondrial genetic differentiation between NZ and SZ, which was indicative of limited genetic exchange between the two areas. However, they also found low nucleotide divergence (0.68%) among the Zanzibar haplotypes, which does not support the argument of no gene flow between NZ and SZ (Särnblad et al., 2011). Female philopatry and male-mediated gene flow is common amongst many cetacean species (Brown Gladden et al., 1997; Palsbøll et al., 1997; Rosel et al., 1999; Wang et al., 1996), including bottlenose dolphins (Krützen et al., 2004). A study of bottlenose dolphins in Shark Bay, Australia found that mtDNA markers vary on a much smaller scale than microsatellite markers, suggesting that female dispersal is considerably smaller than male dispersal (Krützen et al., 2004). Similarly to the study by Särnblad et al. (2011) in NZ and SZ, Krützen et al. (2004) found distinctions in the mtDNA of individuals in two adjacent areas. They also found that interbreeding between the two haplotype clades was occurring, and, based on the fact that no intermediates were found, concluded that the two distinct mtDNA haplotypes could be the result of Shark Bay having been colonized by dolphins with two distinct mtDNA lineages (Krützen et al., 2004). The evidence that mixing is occurring between NZ and SZ and the low nucleotide divergence between NZ and SZ (Särnblad et al., 2011) provide support to reasonably consider that female philopatry and male-mediated gene flow may also occur amongst bottlenose dolphins around Zanzibar Island. Similarly to the dolphins in Shark Bay (Krützen et al., 2004), the ZB dolphins may consist of resident groups of females around NZ and SZ, with males moving between the two areas. Further support to this conclusion is provided in a study of *T. aduncus* in Byron Bay, Australia (Hawkins & Gartside, 2008). Hawkins and Gartside (2008) identified two resident groups of females separated on a microgeographic scale, but, based on social organization, movement patterns, and behavior, concluded that the dolphins in the area should be managed as a single unit (Hawkins & Gartside, 2008). Although evidence points to male-mediated gene flow in ZB, it is well outside the scope of this study to definitively state that this is occurring, and additional studies (genetic and photo-identification) are needed to test this hypothesis.

Both open and closed population models were used to generate an abundance estimate for the bottlenose dolphins around the entire coast of Zanzibar Island. That this study took place over a short period of time (< 2 months), and that the ZB discovery curve (Figure 6) reaches an asymptote, suggest that closed population models are appropriate. However, the assumption of a closed population was

violated by the death of a previously identified individual during the sample period (Hammond, 1986; Otis et al., 1978; Schwarz & Seber, 1999; White et al., 1982). Therefore, the results of the open population models are reported here, and result in a population estimate of 353 (95% CI 290-430) dolphins.

4.3 Population Linkages With Zanzibar's Bottlenose Dolphin Population Unit

Results of this study provide preliminary evidence of population linkage between bottlenose dolphins from ZB and the surrounding areas. This evidence comes in the form of trends in abundance in SZ, and the similarity in whistle characteristics between dolphins from PB and ZB.

Although the most recent estimate is the lowest to date, abundance estimates of the SZ dolphin population were quite stable from 1999-2008 (Table 9) (Öhman, 2010; Stensland et al., 2006; this study). Amir (2010) estimated a removal rate of 7.5-9.6%, which is likely unsustainable given the expected growth rate of < 4% (Moore & Read, 2008; Wade, 1998) and estimated potential sustainable level of take of 2% (Berggren, 2011). The growth rate would likely be even lower in SZ considering the high rate of tourism boats the dolphins are subjected to (Christiansen et al., 2010; Ngazy et al., 2007; Stensland & Berggren, 2007) and the impact they can have (Bejder, 2005; Bejder et al., 2006; Buckstaff, 2004; Christiansen et al., 2010; Nowacek, Wells, & Solow, 2001; Stensland & Berggren, 2007; Williams et al., 2006). Additionally, the removal rate estimated by Amir (2010) is likely an underestimate, as the most recent data shows that 16 dolphins were killed as a result of bycatch in 2007/2008 (Amir, 2010). Given the 2008 abundance estimate, generated in this study, of 120 (95% CI 97-149 dolphins, this corresponds to a 10.7-16.5% removal rate. Berggren (2011) hypothesized that perhaps the area around SZ is ideal for feeding, foraging, and resting, and can therefore significantly increase the expected growth rate. This could enable the population to remain nearly constant, despite the high level of bycatch and impacts due to high tourism intensity. However, it is unlikely that even if the area is ideal, it would raise the expected growth rate high enough to mitigate the large amount of bycatch and effects of heavy tourism use. It is possible that the SZ population remains relatively stable because of migration into the study area, a hypothesis also proposed by Berggren (2011). It is unlikely that animals migrating from NZ alone are able to maintain the stable population numbers in SZ because, similarly to SZ, the amount of bycatch in NZ per year is likely unsustainable (Amir, 2010; Amir et al., 2002; Berggren, 2011). Trends in abundance of dolphins in NZ could provide further insight, but are not identifiable at this stage because abundance of NZ bottlenose dolphins has only been estimated for one year (2008).

Regarding the results of the DFA on dolphins from PB, classification success was moderate (61.8%), suggesting the whistles generated by these bottlenose dolphins do not have as unique characteristics as NZ dolphins, as evidenced by their 86.2% classification success, and even share some of the

whistle structure with ZB animals. Previous studies from SZ, NZ, and PB show that signature whistles of dolphins from all three areas have few inflection points, and, especially in ZB, are comprised of prominently upswept contours (Gridley et al., 2012). Since animals are thought to adjust the sounds they make in response to their environment (Peters, Hemmi, & Zeil, 2007), similarities in acoustic characteristics between distant populations have been suggested to be the result of similar acoustic environments (May-Collado & Wartzok, 2008; Quintana-Rizzo, Mann, & Wells, 2006). For marine mammals, these environments could relate to similarities in bottom composition (Quintana-Rizzo, 2006), presence of certain species, including snapping shrimp (Urick, 1983), or the prevalence of vessel noise (May-Collado & Wartzok, 2008). Given that *T. aduncus* are known to use whistles which avoid masking and attenuation by ambient noise (May-Collado & Wartzok, 2008; Morisaka et al., 2005a), a similar acoustic environment in ZB and PB could explain the similarities in whistle characteristics between dolphins from these two areas; however, further research into the acoustic environments of these areas is needed.

Acoustic mixing may also explain why whistles of PB dolphins do not have as unique characteristics as the NZ population, and even share some of the whistle structure with ZB animals. No migrations over the distance between PB and ZB have been recorded amongst *T. aduncus*, so the likelihood of individuals migrating the 3000 km is low; however, bottlenose dolphins have been found to migrate from Algoa Bay, South Africa (roughly 200 km east of PB) along most of the, and potentially the entire, east coast of South Africa (Reisinger & Karczmarski, 2010). There is a continuous band of *T. aduncus* between PB and ZB (Best, 2007; Hammond et al., 2012; Reisinger & Karczmarski, 2010) and population structures are poorly understood (Natoli, Peddemors, & Hoelzel, 2008; Reisinger & Karczmarski, 2010). Wang et al. (1995b) hypothesize that movement of individuals between adjacent areas could result in similarity in whistles between the areas. Considering the large number of dolphins using the Algoa Bay area (28,482 (95% CI 16,220–40,744)), and their vast migratory patterns (Reisinger & Karczmarski, 2010), it is plausible that they would share whistles with other bottlenose dolphins along the east coast of southern Africa that range further north. In addition to explaining the only moderate classification success of PB whistles, in spite of the large distance between PB and ZB, this hypothesis may also explain why dolphins from SZ are more similar to those from South Africa, with regards to their mtDNA, than to NZ dolphins (Särnblad et al., 2011). Further research is needed on the migratory patterns of bottlenose dolphins along the east coast of southern Africa, including photo-identification, acoustic, and genetic studies, in order to confirm this hypothesis.

4.4 Problems, Constraints, and Suggestions for Future Study

This study has provided evidence that the population structure of Zanzibar Island bottlenose dolphins should not be divided into the north coast and south coast populations, but should rather be considered

as a single population unit, possibly with resident groups of females around the two coasts. Population structures have been identified in bottlenose dolphins from adjacent areas in other locations using distance from shore, group size, occurrence of barnacles, behaviour, colouration (Toth et al., 2012), mtDNA sequencing, microsatellite genotypes (Parsons et al., 2006), and social structure (Gubbins, 2002; Lusseau et al., 2006). Investigating the bottlenose dolphins around Zanzibar Island with respect to one or more of these factors will provide further insight into the population structure of these dolphins. Additionally, increasing the number of sites sampled along the Zanzibar coastline, and returning to these sites multiple times throughout the course of the study, is needed to determine the rate and direction of movement between the two areas.

Furthermore, although evidence suggests the possibility of female philopatry and male-mediated gene flow in the ZB population unit, further genetic studies are needed to confirm this. In addition to genetics, an attempt should be made to identify the sex of the individuals that are found to travel between the north and south coasts. Determining if the individuals travelling between the two areas are male would provide greater insight into the theory of female philopatry and male-mediated gene flow. Dolphin sex can be determined through focusing on the genital area, either visually from photographs, or with an underwater video camera (Lusseau et al., 2003). Also, individuals consistently accompanied by a calf are likely to be mothers, and therefore female (Lusseau et al., 2003).

Further sampling is also needed to confirm the hypothesis put forth in this study that movement into the waters surrounding Zanzibar Island is responsible for the fairly stable population numbers in SZ. Genetic, photo-identification, and acoustic data should be gathered from bottlenose dolphins off the coast of the Tanzanian mainland, Pemba Island, Tanzania, and Zanzibar Island, to determine whether movement is occurring, and to discover the extent of any population linkage.

The population models used in this study use data collected from two different sites, NZ and SZ, to determine an estimate for ZB. Ideally, multi-site population modeling would be used in determining an estimate for ZB, as it includes probabilities for survival, capture, and transitioning between sites (McCrea et al., 2010). The nature of the sampling for this study means that the data cannot be used in multi-site models. For this study, samples were taken from SZ over 19 days, and then NZ for 14. To run multi-site models, each site must be resampled to accurately estimate variables including probability of capturing an individual in a given state, and the probability of transitioning from one state to another at a given time (Cole, 2012; Grosbois et al., 2009; McCrea et al., 2010). In addition, ideally more than two sites would be included (Durban et al., 2005). Sampling in more areas around Zanzibar, especially along the east and west coasts, and returning to all sites multiple times would provide data that is appropriate for multi-site modelling, and result in a more accurate abundance estimate of the bottlenose dolphins around Zanzibar Island.

After running the PCA, a sixth Factor was found to have an Eigenvalue of just less than one (0.92). Based on Kaiser's criterion (Kaiser, 1960), it was not included in the DFA. One variable contributed heavily on Factor 6: number of steps. Although number of steps has been found to explain variability between species of cetaceans (Oswald et al., 2003), it has not, to the author's knowledge, been found to explain variation in dolphin whistles on an intra-specific level. Therefore, although it was considered, it was ultimately not included among the factors used for DFA.

From prior studies (Gridley, 2010; Gridley et al., 2012) 25 acoustic parameters, plus the adopted frequencies, were made available for this study. Number of harmonics was not one of the 25 available parameters, as extracted whistles only included the fundamental frequency. Hawkins (2010) studied different populations of *T. aduncus* around Australia and found the number of harmonics to differ between populations on both a macro and microgeographic level. Future acoustic analysis of whistles from bottlenose dolphins in this area should attempt to include number of harmonics as a variable. This could potentially have an impact on the classification success of the whistles from different populations, and provide further insight into the distribution trends of southern African bottlenose dolphins.

5. Conclusion

The data presented suggest that Indo-Pacific bottlenose dolphins around Zanzibar Island should be considered as a single population unit, at least as it relates to management decisions. Given results from the genetic study by Särnblad et al. (2011), and precedence in the form of the investigations of population structuring in two areas of Australia (Hawkins & Gartside, 2008; Krützen et al., 2004), it is likely that there are resident groups around NZ and SZ. These resident groups are likely to be breeding females, as their dispersal is much less than male dispersal (Krützen et al., 2004). Males are likely moving around the entire island, and interbreeding with both sets of females; however, further research is needed to confirm this conclusion. This study provides the first estimate of the bottlenose dolphin population around Zanzibar Island.

This study also provides evidence, in the form of trends of abundance in SZ, and the results of the acoustic analysis, of a link between dolphins inhabiting Zanzibar Island and neighbouring populations. Further investigation of the bottlenose dolphins around Tanzania (including Zanzibar Island, the mainland coast, and Pemba Island (roughly 50 km north of ZB)) should be performed to determine if there is movement of individuals into and out of the waters surrounding Zanzibar Island, and to determine the speed and direction of movement. These investigations should include photo-identification, genetics, and whistle analysis.

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Appendices

Appendix A—Results of the Huggins Closed Capture Population Models

Huggins closed capture population model outputs including the model used, number of parameters (Np), Akaike's information criterion (AICc), difference between the model in question and the model of best fit (ΔAICc), number of distinct animals ($\widehat{N}$), and total population estimate (N), along with coefficient of variation (CV) and lower (LCL) and upper (UCL) limits at the 95% confidence level. The parameters used in the models are the probability of an individual initially being captured (p), the probability of recapturing an animal that was previous captured (c), and an estimate of capture probability (π). Each parameter was either time dependent (t), constant over time (.), or included a mixture to partition animals into separate groups with similar capture probabilities (m). If the parameter was neither () it was constant and equal to the preceding parameter. Theta values of 0.94, 0.95, and 0.94 were used for NZ, SZ, and ZB respectively, and used to estimate Ntotal.

Model Selection Criteria					**Marked Population**					**Total Population**			
Model	Np	AICc	ΔAICc		$\widehat{N}$	CV	LCL	UCL		N	CV	LCL	UCL
North Zanzibar													
π(.)p(t+m)c()	16	1455.9	0.0		190.1	0.144	153.0	265.5		203	0.156	149	275
p(t)c()	14	1562.0	106.1		120.3	0.017	118.1	126.8		128	0.064	113	145
π(.)p(m)	3	1638.6	182.7		198.7	0.161	156.1	287.9		212	0.172	152	296
p(.)c(.)	2	1722.7	266.8		118.9	0.013	117.4	125.2		127	0.063	112	143
South Zanzibar													
π(.)p(t+m)c()	21	1429.7	0.0		103.7	0.039	98.7	115.5		109	0.072	95	126
p(t)c()	19	1484.0	54.3		97.4	0.017	95.7	103.1		103	0.064	91	116
π(.)p(m)	3	1612.2	182.5		105.3	0.043	99.5	118.3		111	0.075	96	128
p(.)c(.)	2	1627.2	197.5		117.1	0.099	103.4	153.3		123	0.116	98	155
Zanzibar Combined													
π(.)p(t+m)c()	34	3915.2	0.0		237.2	0.060	217.3	275.8		251	0.086	212	297
p(t)c()	33	3981.3	66.1		201.2	0.012	198.2	208.5		213	0.063	188	241
p(.)c(.)	2	4166.7	251.5		382.2	0.243	269.8	665.5		405	0.251	249	657
π(.)p(m)	2	4262.1	346.9		241.0	0.067	218.6	285.3		255	0.091	214	305

Appendix B—Results of the RELEASE Goodness of Fit Tests

Goodness of fit (GoF) test results using the program RELEASE in a time dependent Cormack-Jolly-Seber model in the program R (R Development Core Team) using a POPAN parameterisation. The variance inflation factor ($\hat{c}$), chi-squared statistic (x^2), degrees of freedom (df), and statistical significance (p-value) are all measured in the GoF test.

Test	$\hat{c}$	x^2	df	p**-value**
North Zanzibar				
Test 2 + Test 3	3.27	107.96	33	< 0.01
Test 2	4.05	81.06	20	< 0.01
Test 3	2.07	26.90	13	0.01
Test 3.SR	3.39	23.74	7	< 0.01
Test 3.Sm	0.53	3.16	6	0.79
South Zanzibar				
Test 2 + Test 3	2.84	110.90	39	< 0.01
Test 2	4.35	100.07	23	< 0.01
Test 3	0.67	10.83	16	0.82
Test 3.SR	0.82	6.59	8	0.58
Test 3.Sm	0.53	4.24	8	0.84
Zanzibar Combined				
Test 2 + Test 3	3.52	310.01	88	< 0.01
Test 2	4.57	278.96	61	< 0.01
Test 3	1.15	31.05	27	0.27
Test 3.SR	1.98	25.83	13	0.02
Test 3.Sm	0.37	5.22	14	0.98

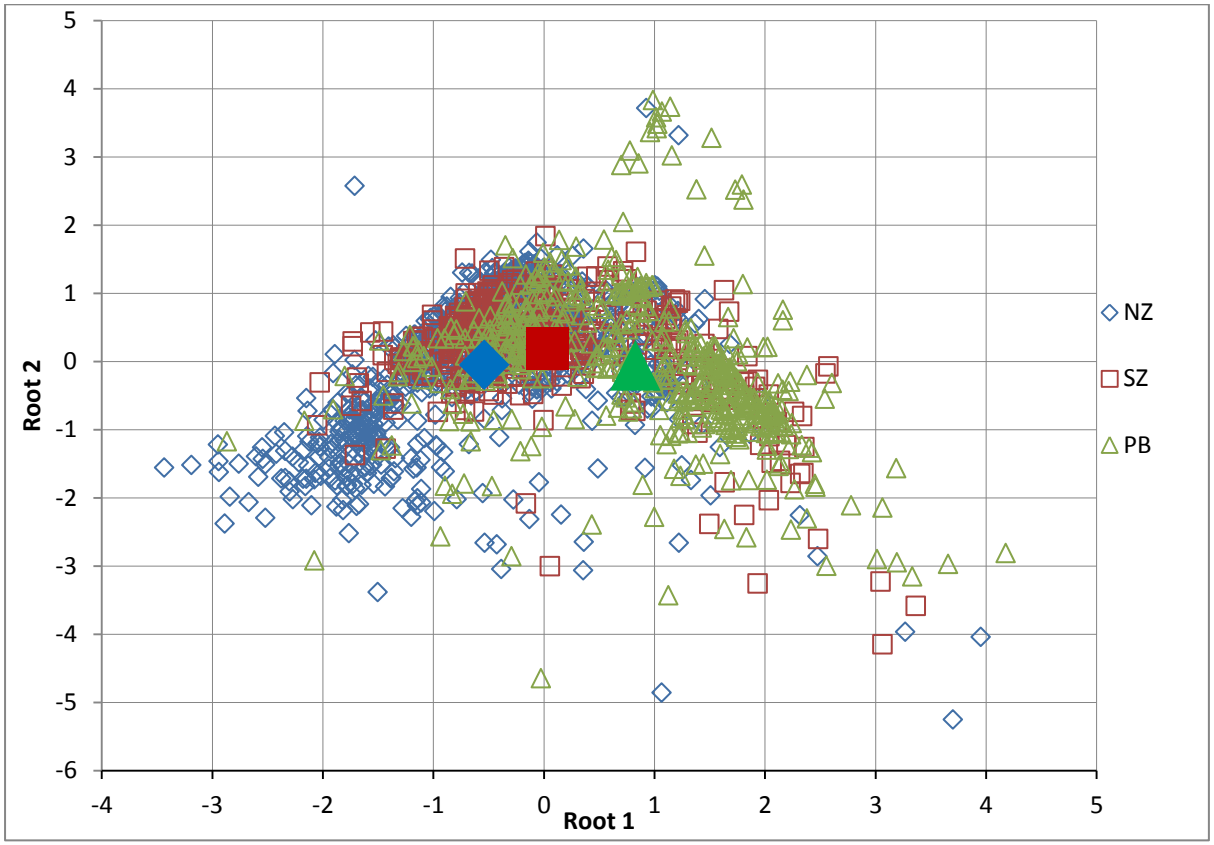
Appendix C— Results of the Open Population Models

Open population POPAN model outputs. Model parameters could be time dependent (t) or constant (.), and include: the probability that an individual will survive between two sampling occasions (Φ), the probability of capture at a given occasion (p), the probability of an animal entering the study area between subsequent sampling occasions (b), and the super population (N), an estimate of the total number of individuals, captured and uncaptured, in the study area. Outputs included number of parameters (Np), quasi-Akaike's information criterion (QAICc), difference between the model in question and the model of best fit (ΔQAICc), Akaike weight (Weight), the amount the model deviates from perfect fit (QDev), the number of distinct animals ($\hat{N}$), coefficient of variation (CV), lower (LCL) and upper (UCL) 95% confidence limits, and the total population estimate (N). QAICc and ΔQAICc were corrected based on the $\hat{c}$ scores of 3.27 (NZ), 2.84 (SZ), and 3.52 (ZB), and total population numbers were calculated using θ values of of 0.94, 0.95, and 0.94 for NZ, SZ, and ZB respectively.

	Model Selection Criteria						Marked Population					Total Population			
Model	Np	QAICc	ΔQAICc	Weight	QDev		$\hat{N}$	CV	LCL	UCL		N	CV	LCL	UCL
North Zanzibar															
Φ(t)p(t)b(.)N(.)	17	354.6	0.0	0.96	70.9		137.8	0.047	125.7	151.1		149	0.078	128	173
Φ(t)p(t)b(t)N(.)	21	361.0	6.4	0.04	68.3		142.8	0.056	128.0	159.2		154	0.083	131	182
Φ(.)p(t)b(.)N(.)	17	374.7	20.1	0.00	91.0		139.6	0.050	126.7	153.7		151	0.079	129	176
Φ(.)p(t)b(t)N(.)	20	378.9	24.3	0.00	88.5		140.2	0.051	127.0	154.8		151	0.080	129	177
Φ(t)p(.)b(t)N(.)	8	3840	29.4	0.00	119.6		149.8	0.063	132.5	169.4		161	0.088	136	192
Φ(t)p(.)b(.)N(.)	4	387.9	33.3	0.00	131.8		134.5	0.042	123.9	146.0		145	0.075	125	168
Φ(.)p(.)b(.)N(.)	4	403.5	48.9	0.00	147.4		139.6	0.047	127.4	152.9		151	0.077	130	175
Φ(.)p(.)b(t)N(.)	7	403.8	49.2	0.00	141.6		153.4	0.065	135.0	174.3		165	0.089	139	197
South Zanzibar															
Φ(.)p(t)b(.)N(.)	22	410.6	0.0	0.59	95.9		112.9	0.061	100.3	127.1		119	0.086	101	141
Φ(.)p(t)b(t)N(.)	26	411.7	1.0	0.36	87.5		113.0	0.138	86.3	147.9		119	0.151	89	160
Φ(t)p(t)b(t)N(.)	29	416.1	5.4	0.04	84.6		104.1	0.038	96.6	112.2		110	0.072	95	126
Φ(t)p(t)b(.)N(.)	26	417.7	7.0	0.02	93.5		110.3	0.055	99.0	122.8		116	0.082	99	137
Φ(.)p(.)b(t)N(.)	9	428.1	17.5	0.00	142.3		109.7	0.048	99.9	120.4		116	0.078	99	135
Φ(t)p(.)b(t)N(.)	16	428.3	17.7	0.00	127.3		109.5	0.060	97.4	123.1		115	0.086	98	136
Φ(t)p(.)b(.)N(.)	8	433.1	22.5	0.00	149.4		122.3	0.058	109.2	137.1		129	0.084	109	152
Φ(.)p(.)b(.)N(.)	4	440.4	29.7	0.00	165.0		115.4	0.057	103.2	129.0		122	0.084	103	143

Zanzibar Combined															
Φ(t)p(t)b(t)N(.)	43	727.5	0.0	1.00	132.3		333.6	0.079	285.6	389.6		353	0.100	290	430
Φ(t)p(.)b(t)N(.)	15	760.3	32.8	0.00	226.4		255.8	0.077	219.8	297.6		271	0.099	223	329
Φ(.)p(t)b(t)N(.)	42	768.1	40.6	0.00	175.2		256.7	0.044	235.6	279.7		272	0.075	234	315
Φ(t)p(t)b(.)N(.)	40	774.2	46.7	0.00	185.9		249.1	0.040	230.5	269.2		264	0.073	229	304
Φ(.)p(.)b(t)N(.)	12	798.3	70.9	0.00	270.7		251.2	0.039	232.7	271.1		266	0.073	231	307
Φ(.)p(t)b(.)N(.)	36	802.1	74.6	0.00	222.8		255.2	0.039	236.4	275.6		270	0.073	234	312
Φ(t)p(.)b(.)N(.)	10	819.1	91.7	0.00	295.6		247.6	0.035	231.0	265.3		262	0.071	228	301
Φ(.)p(.)b(.)N(.)	4	844.3	116.8	0.00	333.1		254.8	0.038	236.5	274.4		270	0.072	234	311

Appendix D—Canonical Scores From The Discriminant Function Analysis



Plot of the canonical score results from the DFA. Values from NZ are denoted with blue diamonds, SZ with red squares and PB with green triangles. Group centroids are represented by larger, solid-coloured shapes of the same shape and colour.